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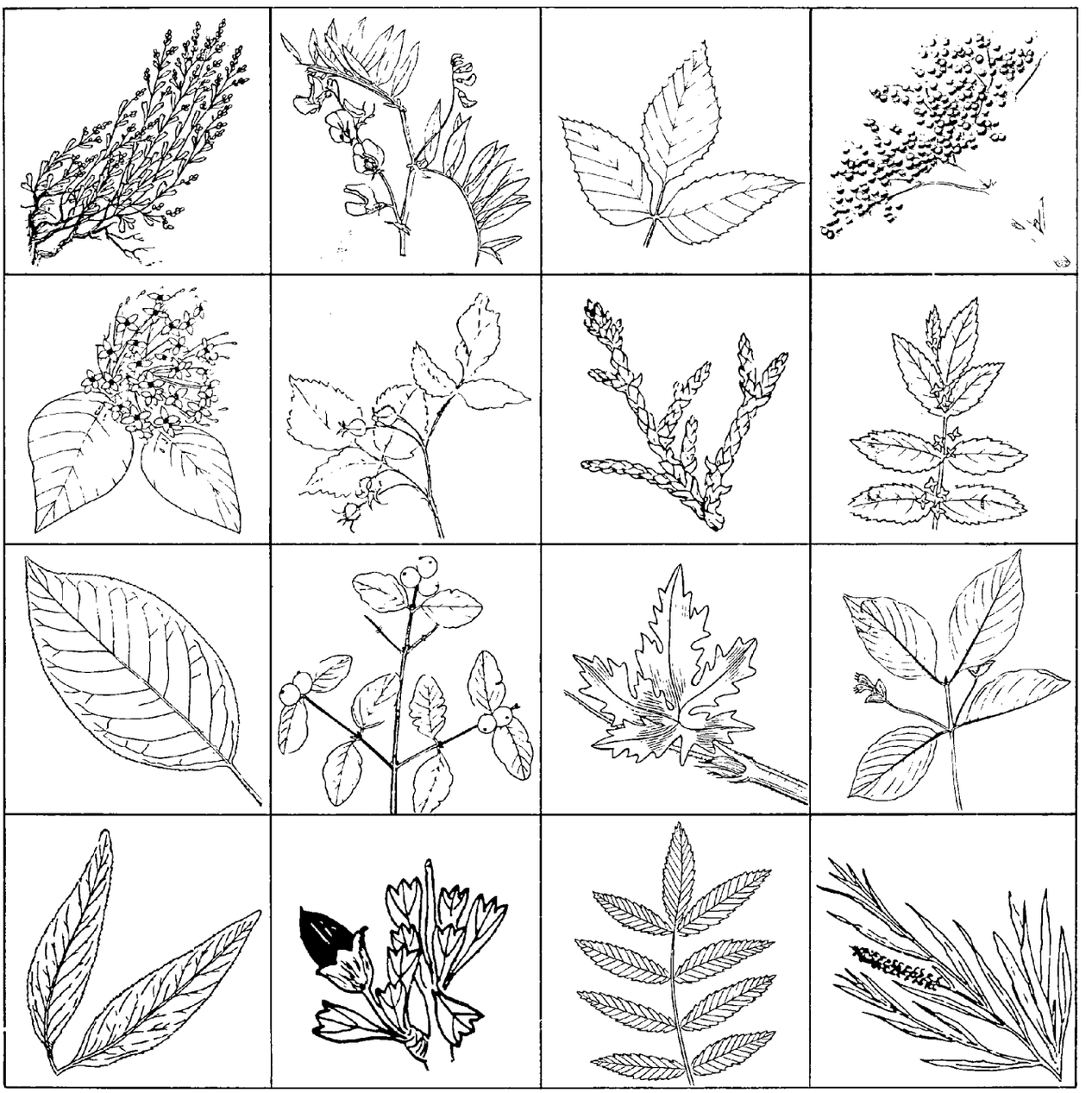
Wildland Shrubs
-Their Biology and Utilization

AN INTERNATIONAL SYMPOSIUM UTAH STATE UNIVERSITY · LOGAN, UTAH · JULY 1971



USDA Forest Service General Technical Report INT-I, 1972
INTERMOUNTAIN FOREST AND RANGE
EXPERIMENT STATION
Ogden, Utah 84401

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USDA Forest Service
General Technical Report INT-I
August 1972

Wildland Shrubs -Their Biology and Utilization

An International Symposium
Utah State University
Logan, Utah
July 1971

Technical Editors:
Cyrus M. McKell
James P. Blaisdell
Joe R. Goodin

INTERMOUNTAIN FOREST AND RANGE EXPERIMENT STATION
Forest Service
U. S. Department of Agriculture
Ogden, Utah 84401
Robert W. Harris, Director

Foreword

Why Is a Shrub Symposium Needed?

The answer to this question is obvious in view of the great volume of research that has been done with grasses and forbs while, in contrast, there has been considerably less research and development of shrubs. Yet, shrubs offer tremendous potentials for man's benefit in making the arid and semi-arid lands of the world more productive and useful. In light of the great range of adaptation possessed by shrubs as a group, it is quite amazing that they have escaped intensive study to the same degree as other plant groups. Shrubs range from some of the highest mountain elevations to the lowest. They extend from the foothills out into the drier desert areas where most grasses fail to accompany them. Only the ephemeral opportunistic annual grasses and forbs are the associated species for many shrub communities in desert and saline areas. Even under such conditions, shrubs offer certain advantages because of their productivity, palatability, nutritional qualities, value as wildlife habitat, cover for the soil, and general role in ecosystem functioning. Therefore, a Symposium focusing on the use and biology of shrubs is a vital necessity to discuss what is known and determine what is not known and to suggest plans for work that will bring greater benefits to mankind by using and understanding the potentials that exist in shrub communities worldwide.

The State of Utah is a logical place to hold this International Shrub Symposium. Some of the early beginnings in the field of Range Management took place on the Wasatch Plateau and in the institutions in this State. These include the Forest Service and Utah State University. Over the years, research on shrubs has occupied a small but important role in the studies undertaken in the field of range management. Many references will be made to the principal shrub communities that exist in this area.

Specific Purposes of the Symposium

Several major objectives were set for the Symposium. One, to review existing and scattered literature available on the biology and utilization of shrubs. Second, to bring together scientists, both as speakers and listeners, to discuss research and applications and to exchange ideas and experiences. Third, to identify needed areas of research. Fourth, to look for new uses of shrubs that would better utilize the potential shrubs possess in many different situations. A fifth objective is to assemble in the proceedings a review of the important aspects of shrub biology and utilization for use throughout the world. And finally, to develop plans for future work.

Much of the published work on shrubs is often difficult to find because of the way in which it is classified. Specific work may

often deal with a physiological or ecological aspect in a particular community or with a given species, but cannot be found easily by going to an index using only the word "shrub." However, this is perhaps the only avenue that is available in most cases to the researcher. Monographs on individual shrubs have been produced and are extremely valuable. Overall reviews on useful shrubs are very limited in their occurrence; for this reason, this proceedings will fill a vital need in the world literature on shrubs.

The outlook on shrubs at this Symposium is positive. Instead of looking for ways to control shrubs by using chemicals, bulldozers, or burning, we seek to understand enough of the biology of shrubs to permit better utilization of their favorable characteristics or to replace those that are less desirable with shrubs having desirable characteristics.

Sections of the Proceedings

The proceedings is organized into eight sections.

In the section on Continental Aspects of Shrub Distribution, Present Utilization, and Potential for the Future, the authors present an overview of the worldwide pattern of shrub occurrence and how various shrub species are used by man or his animals. Some of these uses have been in existence from antiquity while others may be more recent and have occurred in response to necessity or developing local customs.

In the section on Present and Possible Uses of Shrubs, specialists describe specific ways in which shrubs presently find use in a multitude of situations. Whereas the more traditional concepts of shrub use concern their feed value for livestock or wildlife, shrubs also offer tremendous potentials for low maintenance landscaping in nonirrigated areas such as interstate highways and for their value as soil cover and stabilization. In some countries it is possible to harvest shrubs and other associated species for livestock fodder. The paper titled "Fire Relations" presents new concepts in shrub characteristics that lend slow burning features to some shrubs and make them valuable as replacement species in areas of high fire hazard.

Genetics is probably one of the most neglected areas in the biology of shrubs. The section on Genetic Potential presents discussions on the evolution and diversity of arid land shrubs. Many interesting types could be selected based on field observations of their performance under stress conditions and palatability to both domestic livestock and wildlife. The final paper in this section considers some of the ways in which ornamental shrubs have been developed by making use of the great amount of variability that has been discovered by ornamental horticulturists.

The section on Synecology provides a background of information and approaches to the study of shrubs in natural communities. A major objective is to provide a better understanding of how shrubs respond to grazing use and to some of the more critical factors of the environment plus how they perform an important role in the ecosystem by recycling nutrients. The ecological impact of animal selectivity and the effects of insects and diseases on shrubs are also discussed in the context of community dynamics.

Shrub Physiology is an area that will require a great deal more study in order to provide land managers with an understanding of shrub responses and characteristics. One area of real concern is the adaptation of shrubs to moisture and salinity stress.

Shrubs also possess rather interesting adaptations with regard to their photosynthetic activity and efficiency in both the mobilization and the storage of carbohydrates that give them special capabilities in desert conditions. The final chapter in the physiological section deals with bud activa-

tion, an area in which shrubs show unique responses to utilization.

The section on Nutritive Quality includes valuable information on various aspects of food values of shrubs. Several chapters elucidate the nutritive value of shrubs for domestic livestock, for wildlife, and for a particularly interesting animal, the goat.

The section on Regeneration and Establishment of shrubs provides new ideas for obtaining seeds and establishing shrubs in such diverse habitats as foothill game range and saline basins. Because shrubs are found under such difficult environmental conditions, two papers discuss means by which shrubs can be established by modifying the seedling environment.

The final section of the proceedings is on a more philosophical level in which some of the future opportunities for using shrubs in arid lands are covered by scientists who have a broad background and world understanding of shrublands and some of the potentials that these lands may hold for future generations.

A large measure of credit for the success of the Symposium is due to those who served on the planning committee with me. They are as follows:

Dr. James P. Blaisdell, Assistant Director, Intermountain Forest and Range Experiment Station, USDA Forest Service, Ogden, Utah

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Dr. Floyd Kinsinger, Acting Chief, Technical Services Division, Denver Service Center, Bureau of Land Management, Denver, Colorado

Dr. John Neuhold, Director, Ecology Center and Professor of Wildlife Management, Utah State University, Logan, Utah

Dr. Wayne B. Ringer, Director, Conference and Institute Division, Utah State University, Logan, Utah

Dr. Neil E. West, Associate Professor of Range Science, Utah State University, Logan, Utah

Major financial and administrative support for the Symposium was provided by the Ecology Center, Utah State University; the Agricultural Experiment Station, Utah State University; USDA Forest Service, Intermountain Forest and Range Experiment Station; and the Rockefeller Foundation. Other support for the Symposium in the form of travel assistance was received from the Smithsonian Institution, Ford Foundation, USDA Agricultural Research Service, USDI Bureau of Land Management, CSIRO, FAO, the Society for Range Management, and various universities.

DR. CYRUS M. McKELL
General Chairman of Symposium and Professor and Head, Range Science Department, Utah State University, Logan, Utah

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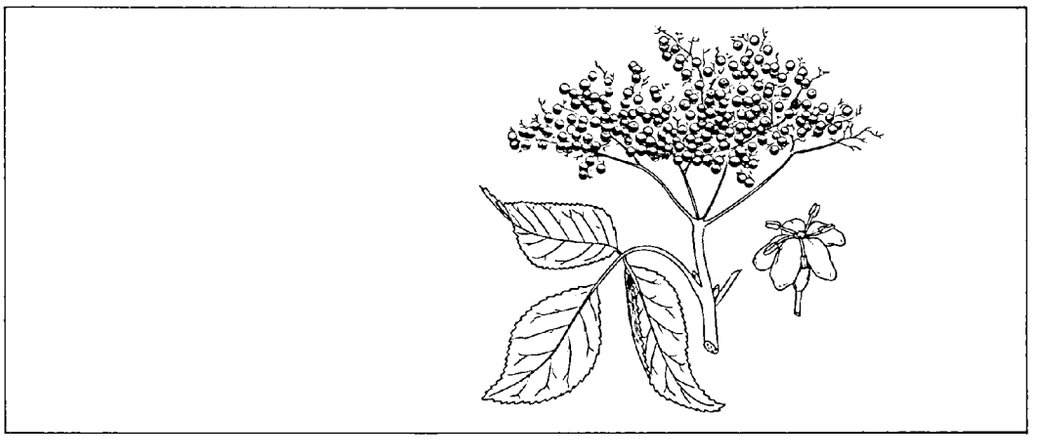

Section I.

Continental Aspects of Shrub Distribution, Utilization, and Potentials

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Indian subcontinent

K. M. M. Dakshini

Department of Botany, University of Delhi, Delhi-7, India

The circular announcing this International Symposium stated "There is an increasing awareness that man has given but scant attention to the usefulness of shrubs for animal feed, soil consumption, low maintained landscaping, and industrial products as he has attempted to increase the productivity of the world's dry lands. Shrubs have many excellent characters to offer that have been either ignored or considered a problem." This statement is very true when we take into consideration the arid and semiarid regions of our country and the shrubs that inhabit them. However, with the establishment of the Central Arid Zone Research Institute at Jodhpur, India, and a similar Institute in Pakistan, an advance has been made in the effort to evaluate the potential of shrubs in dry regions of the Indian subcontinent. In the following pages, therefore, a brief review of work done so far is offered with a view to assessing and evaluating the existing information on shrub biology with particular reference to the Indian subcontinent.

Delimitation, distribution, and characteristics of arid and semiarid regions

In the past, arid and semiarid regions were defined on the basis of climatic factors alone (Köppen 1923; Mathews 1931; Lang 1920; de Martonne 1905; Thornthwaite 1948; Transeau 1905; Emberger 1930; Gorczynski 1943; Stenz 1946; Boyko 1949); accordingly, Köppen's world map included Thar and Rajasthan under desert climate and the surrounding portion that extends up to Cutch and Gujarat, and certain parts of Madras are included under Steppe climate. However, since vegetation is the result of the response of plants to many variables of the climatic factors, no single factor can characterize deserts or arid and semiarid regions. Pramanik, Hariharan, and Ghose (1952) defined deserts or arid regions of India as areas having rainfall of 10 inches or less and a mean annual diurnal temperature range of 24° F. or more; they defined semiarid regions as areas having rainfall ranging from 10 to 20 inches and an annual diurnal temperature range of 18° F. or more. However, a correlation of climate and vegetation led Bharucha (1955) to retain as the limit of the arid zone the 10 inches isohyet, while the limit of the semiarid zone at the 30 inches isohyet. On the basis of these criteria as well as those of Thornthwaite (1948), the areas of arid and semiarid zones in India total 317,090 sq. km. and 956,750 sq. km., respectively (table 1); this excludes the cold desert of Jammu and Kashmir State, which contains 70,300 sq. km. of arid and 13,780 sq. km. of semiarid areas (Krishnan 1969). Figure 1 gives the distribution and delimitation of these zones. In the North, next to Rajasthan, Gujarat has the largest area within the arid zone. In South India, the arid region is mainly confined to a portion of Rayalaseema region in Andhra Pradesh (fig. 1) and adjoining parts of Mysore. Of the semiarid zone, 59 percent is situated in peninsular India. The whole of western Pakistan, i.e., Baluchistan, Sind, Thar, Punjab, and Waziristan, however, comes under the delimitation of the arid zone (fig. 2). However, this distinctness between the arid and semiarid zones is not so well marked when temperatures

Table 1.--*Distribution of area of arid and semiarid zones of India by States (Krishnan 1969)*

State	Area		Area distribution	
	Arid	Semiarid	Arid	Semiarid
	Sq. km.		*Percent*	
Andhra Pradesh	21,550	138,670	7	15
Gujarat	62,180	90,520	20	9
Haryana	12,840	26,880	4	3
Madhya Pradesh	--	59,470	--	6
Madras	--	95,250	--	10
Maharashtra	1,290	189,580	0.4	19
Mysore	8,570	139,360	--	15
Punjab	14,510	31,770	5	3
Rajasthan	196,150	121,020	61	13
Uttar Pradesh	--	64,230	--	7
Total	317,090	956,750		
Jammu and Kashmir cold desert	70,300	13,780		

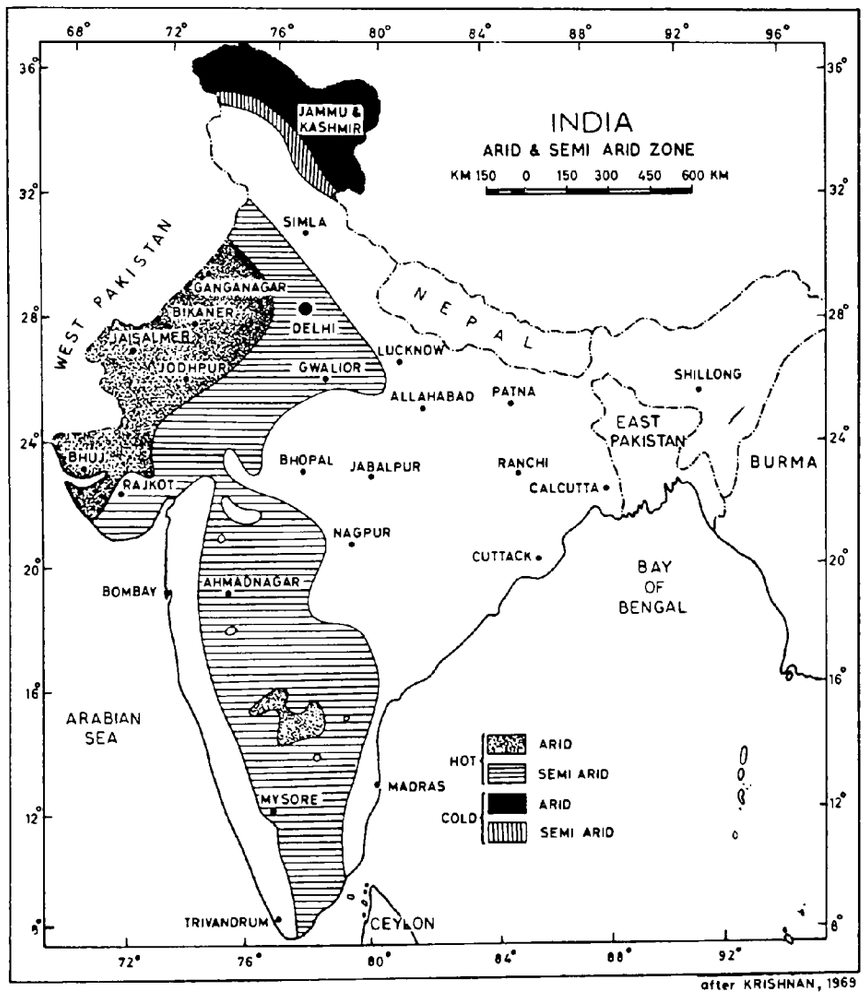
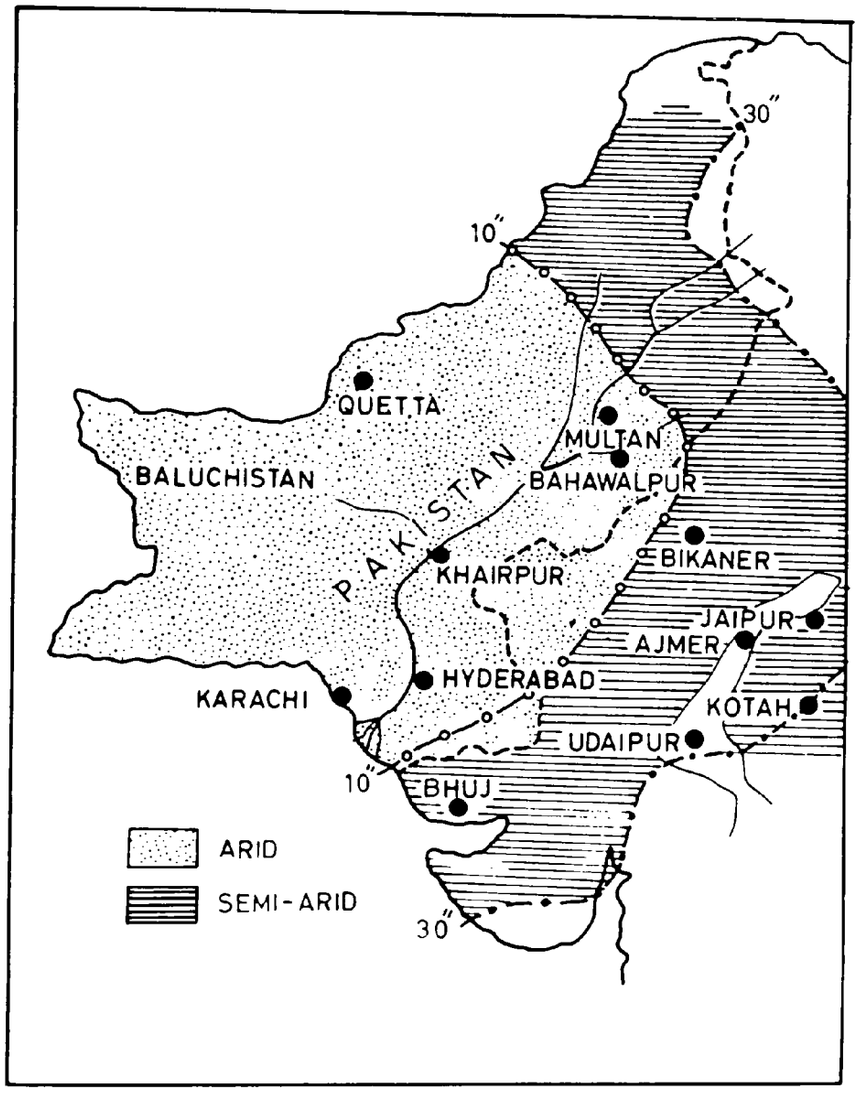


Figure 1.--Distribution of arid and semiarid zones in India.



after BHARUCHA, 1955

Figure 2.--Distribution of arid and semiarid zones in western Pakistan and northwest India.

during different seasons are considered. The cold desert of Jammu and Kashmir, with an annual temperature range of 14°-32° C., has July as its hottest month and January/February as its coldest month. For the remaining areas of arid and semiarid zones the hottest month is May, except for some areas in the South where April is even hotter. The mean maximum temperature in these zones during the hottest month varies from 40°-42° C. except in some coastal regions, which are cooler. The coldest month (in the North) is January, but December is coldest in many regions in the South; and the minimum temperatures during the coldest month vary from 3° C. to 5° C. in Punjab, to 18° C. to 24° C. in Madras.

Tables 2 and 3 give comparative data on normal annual rainfall, potential evapotranspiration, water deficiency, and aridity index in various arid and semiarid areas of the Indian Territory. Such values are not available for arid regions of Pakistan, but it is assumed that they would be identical to those of adjacent arid regions of India.

Table 2 indicates that arid zones of northwest India (Rajasthan, Punjab, Haryana, and Gujarat) are more arid than a few patches of arid zones in peninsular India. However, the highest aridity index is for the cold desert of Jammu and Kashmir.

Similarly, from table 3 it is apparent that semiarid zones in Rayalaseema and Bellary/Bijapur regions have higher aridity index numbers. However, in these semiarid zones also, the highest aridity index is for the Kargil region in Ladakh district of Jammu and Kashmir State.

Table 2.--*Normal annual rainfall, potential evapotranspiration, water deficiency, and aridity index in arid zones of various States of India (Krishnan 1969)*

State	Normal rainfall	Mean annual potential evapotranspiration	Mean annual water deficiency	Mean aridity index[1]
	Mm.			*Percent*
Andhra Pradesh	544	1,700	1,156	68
Gujarat	473	1,492	1,091	68
Haryana	356	1,527	1,171	76
Jammu and Kashmir	94	527	433	83
Mysore	503	1,563	1,060	68
Punjab	335	1,411	1,076	76
Rajasthan	319	1,473	1,156	78

[1]The aridity index is the ratio between the annual water deficiency and the annual water need expressed as a percentage.

Table 3.--*Normal annual rainfall, potential evapotranspiration, water deficiency, and aridity index in semiarid zones in various States of India (Krishnan 1969)*

State	Normal rainfall	Mean annual potential evapotranspiration	Mean annual water deficiency	Mean aridity index
	Mm.			*Percent*
Andhra Pradesh	674	1,723	1,049	61
Jammu and & Kashmir	241	678	437	65
Madras	917	1,756	859	48
Maharashtra	712	1,515	802	53
Mysore (Bellary, Bijapur)	599	1,457	858	59
Rajasthan	776	1,397	621	55

General vegetation and distribution of shrubs

The vegetation of arid and semiarid regions generally is xerophytic and may be classified either according to rainfall (i.e., species occurring in areas that receive from 5 to 10, 10 to 20, and 20 to 30 inches of precipitation per year), or on the basis of edaphic variations. Plant communities within each area are less varied in composition and number of plant species. The flora is represented by 40 families of Phanerogams, and the ratio of genera to species is 1:1.6. The shrubs belong to the families Leguminosae, Malvaceae, Asclepiadaceae, Capparaceae, Euphorbiaceae, and Ephedraceae.

Classification of vegetation on the basis of habitat was suggested by Biswas and Rao (1953); however, a detailed systematic treatment was suggested more recently by Champion and Seth (1963). The entire vegetation of regions in India has been classified under two major types:

1. Dry deciduous type
2. Tropical thorn forest

The majority of subtypes in these two major types have been designated as edaphic climax, though transitory successional stages are also indicated. An outline of this classification with characteristic plant species and distribution follows. The shrub species in each type or subtype are marked with an asterisk.

Dry Deciduous Type

Distribution: Mostly in northwestern India.....semiarid type

Main type: *Anogeissus pendula*

Storey	Characteristic plant species
I.	*Acacia catechu, A. latifolia, A. leucophloea, Aegle marmelos, Butea monosperma, Diospyros tomentosa, Sapindus emarginatus, Azadirachta indica, Zizyphus gleberrima.*
II.	*Dichrostachys cineraria, Grewia tenax, Zizyphus mauritiana.*
III.	**Grewia flavescens, *G. tenax, *Flacourtia sepiaria, *Gymnosporia spinosa *Securinega leucopyros, *Rhus mysurensis, *Balanites aegyptiaca, *Capparis decidua, *C. sepiaria, *Adhatoda vasica, *Lepidagathis cristata, *Zizyphus nummularia, *Cassia auriculata, *Carissa opaca.*
IV.	Grasses

Subtype: Saline/alkaline scrub savannah

a) *Phoenix* Savannah:

*Butea monosperma, Salvadora persica, *Carissa opaca.* Grasses: *Desmostachya bipinnata, Vetiveria zizanioides.*

b) Babul Savannah:

*Acacia arabica, A. leucophloea, Salvadora persica, S. oleoides, *Capparis decidua, *C. sepiaria,* and grasses.

c) *Salvadora--Tamarix:* (Western U.P., Punjab, Rajasthan, Saurashtra)

*Acacia arabica, Salvadora persica, S. oleoides, *Capparis decidua, *C. sepiaria, *Randia dumatorum, *Calotropis procera, *Kochia indica, Sueda fruticosa, Salsola foetida.*

Tropical Thorn Forest

I. Southern Tropical Thorn Forest

Distribution: M.P., Maharashtra, Madras, Mysore...semiarid type

a) Southern thorn forest:

*Dichrostachys cineraria, Zizyphus mauritiana, Mimosa hamata, *Calotropis procera, Acacia catechu, A. leucophloea, Anogeissus pendula, Azadirachta indica, Bahunia racemosa, *Flacourtia indica, *Randia dumetorum, *Zizyphus nummularia, *Gardenia* spp., *Santalum album, Strychnos nux-vomica, *Ixora* spp., **Canthium dicoccum, *Dodonaea viscosa, *Capparis decidua, *Zizyphus oenoplia, *Lantana* spp., **Atlantia monophylla.*

b) Carnatic umbrella thorn forest:

*Acacia planifrons, Albizzia amara, Chloroxylon swietiana, Dichrostachys cineraria, Dalbergia spinosa, *Zizyphus nummularia.*

c) Southern thorn scrub:

*Albizzia amara, chloroxylon swietiana, Wrightia tinctoria, Zizyphus xylophyros, *Capparis decidua, *Securinega leucopyros, *Randia dumetorum, *Canthium dicoccum, Pterolobium indicum, *Acacia pennata.*

d) Southern *Euphorbia* scrub....arid type:

**Euphorbia antiquorum, *E. tirucalli, *Capparis decidua, *Dodonaea viscosa, *Cassia auriculata, *Barleria buxifolia, *Opuntia dillenii.*

II. Northern Tropical Thorn Forest

a) Desert thorn forest:

Distribution: Punjab, Rajasthan, Gujarat....arid to semiarid

*Acacia senegal, Prosopis specigera, Salvadora oleoides, *Calotropis gigantia, *C. procera, *Zizyphus nummularia, *Tephrosea purpurea, *Calligonum polygonoides, *Leptadenia pyrotechnica, *Crotalaria bruhia, *Aerva javanica, Holoptelia integrifolia, *Flacourtia indica, Tecomella undulata, *Gymnosporia spinosa, *Hesperethusa crenulata, *Euphorbia nivulia, *Acacia jacquimontia, *Grewia pilosa, *Capparis zeylanica, *Sericostemma pauciflora, Cordia rothii, *Euphorbia neriifolia,*Balanites aegyptiaca, Commiphora mukul, Premna integrifolia, *Grewia tenax, Salvadora persica, *Barleria prionites, *Peristrophe bicalyculata, *Justicia heterocarpa.*

b) Ravine thorn forest:

Distribution: Rajasthan, Western U.P.,....semiarid

**Capparis decidua, *C. zeylanica, *Carissa spinarum, *Calotropis procera, *Adhatoda vasica, *Zizyphus* spp.

c) *Zizyphus* scrub:

Distribution: Western Rajasthan, Pakistan....arid (rocky intermingled with *Euphorbia* Type; intense biotic pressure)

*Acacia leucophloea, Dichrostachys cineraria, *Zizyphus nummularia, Acacia senegal, Anogeissus pendula, Prosopis specigera, *Securinega leucopyros.*

d) Tropical *Euphorbia* scrub

Distribution: Western Rajasthan, Paksitan, Kutch....arid

**Euphorbia neriifolia, *Grewia tenax, *Barleria acanthoides, *Aerva javanica, *Sarcostemma acidum, *Rhus mysurensis, *Adhatoda vasica, *Capparis decidua, *Cocculus hirsutus, *Gymnosporia spinosa, Premna mucronata, *Indigofera cordifolia, *Euphorbia antiquorum, *Fagonia cretica, *Arthrocnemum indicum.*

e) Miscellaneous edaphic type:

*Tamarix ericoides, *Calotropis procera, Acacia senegal, Salvadora persica, *Cassia auriculata*

A survey of these two major vegetational types common to arid and semiarid zones of the Indian subcontinent indicates that the Dry Deciduous type is mostly semiarid and is confined to the northwest of the subcontinent and mostly confined to India. In this complex of vegetation, trees predominate and the shrubs form the important second or third tier of the stand. On the other hand Tropical Thorn forests are spread throughout the arid and semiarid regions of the continent. Southern regions of this type are on more gravelly substratum; here the shrubs are sparse in comparison to the northern counterpart. In the southern region, tree tier and the ground cover (of grasses) predominate, whereas in the northern region, though the vegetation is sparse and open, the shrub tier is dominant and the herbaceous ground cover is seasonal.

Table 4.--*Shrubs of arid and semiarid regions of the Indian subcontinent*

Arid		Semiarid	
South	North (including Pakistan)	South	North
Barleria buxifolia	*Aerva tomentosa*	*Acacia pennata*	*Adhatoda vasica*
Calotropis procera	*Arnebia hispidissima*	*Canthium dicoccum*	*Alhagi pseudalhagi*
Capparis decidua	*Arthroenemum indicum*	*Capparis divaricata*	*Arnebia hispidissima*
Cassia auriculata	*Barleria prinoites*	*Dodonea viscosa*	*Calotropis gigantea*
Dodonea viscosa	*Calligonum polygonoides*	*Flacourtia indica*	*C. procera*
Euphorbia tirucalli	*Calotropis gigantea*	*Ixora*	*Capparis decidua*
Opuntia dillenii	*C. procera*	*Lantana camara*	*C. sepiaria*
	Capparis zeylanica	*Pterolobium indicum*	*Carissa spinarum*
	Crotolaria burhia	*Securinega leucopyrus*	*Cassia auriculata*
	Euphorbia antiquorum		*Farsetia macrantha*
	E. neriifolia		*Flacourtia sepiaria*
	E. nivulia		*Grewia aspera*
	Fagonia cretica		*G. tenax*
	Farsetia macrantha		*G. villosa*
	Flacourtia cataphracta		*Gymnosporia spinosa*
	Hesperithusa crenulata		*Lagerstroemia parviflora*
	Leptadenia pyrotechnica		*Lepidagathis cristata*
	Maerua arneria		*Lycium barbarum*
	Opuntia dillenii		*Mimosa rubicaulis*
	Pluchea lanceolata		*Premna integrifolia*
	Salsola baryosma		*Rhus mysurensis*
	Salvia aegyptiaca		*Securinega leucopyrus*
	Sarcostemma acidum		*Zizyphus mauritiana*
	S. paucifolia		*Z. nummularia*
	Tamarix dioica		
	Tephrosea purpurea		
	Zizyphus nummularia		

Arid regions, both in north and south of our country and those of western Pakistan as well, have similar physiognomy and vegetational composition, i.e., *Euphorbia* scrub. However, the northern arid regions are richer in components than the south. Another important point to note is the fact that owing to the contiguity of drier and more arid regions of the west, the arid region of the north has more western and central European elements in the flora. The southern arid region, on the contrary, is surrounded by a semiarid type of vegetation and therefore has more Indian elements in the flora. The various shrub species in the arid and semiarid regions of the Indian subcontinent are listed in table 4.

Utilization and potentials

Diversity of habitats in the arid and semiarid regions creates a condition of high adaptive and selective potential in plants. Since shrub species form the perennial plant cover, the phenomenon of behavioral evolution is significant. An assessment of this trait of shrub species goes a long way in the improvement of the plant species, harnessing the environmental potentialities and making the arid and semiarid lands more productive and more useful to mankind. It is with a view to present information on the behavior and metabolism in relation to habitats, economic uses, and indicator values of some of the common shrub species that existing information is summarized below.

Behavior and metabolism

Zizyphus nummularia, a common undershrub, is found throughout arid and semiarid regions, also on sandy and rocky substratum. The fresh fruits are edible, and dried fruits in the form of powder form a staple of diet for the local population during periods of scarcity of food. Also, the tender shoots and leaves are the only food available for sheep and goats during summer months. Table 5 gives data on morphology of the plant parts in relation to habitat.

The plant species found on sandy substratum produce larger fruits and more pulp than species growing on the rocky substratum. However, the rocky substratum seems to favor development of leaves as the average length of the leaf in the rocky habitat is substantially longer than that for species that flourish on sandy habitat. This can be an indicator to a pasture development program.

Similar effects of the habitat and microenvironmental factors on the metabolism of the plant can be noted from table 6. Table 6 shows that plants in sandy habitats produced maximum acid synthesis during the summer season whereas plants in rocky habitats synthesized most acid during the rainy season. Younger stems and leaves show higher TAN values than older plant parts. Further analysis of the major acid types indicates that concentration of malic acid in leaves and stems increases as drought increases.

Table 5.--*Effect of habitat on growth forms of* Zizyphus nummularia *(Nanda 1967)*

Habitat	Shape of leaves	Average length of leaves	Shape of seeds	Average diameter of fruit		Weight of 100 fruits		Weight of pulp of 100 fruits
				Ripe	Unripe	Ripe	Unripe	
		Cm.		*Mm.*		*G.*		
Sandy	Orbicular	5.23	Oblong	11.19	8.78	86.80	40.60	62.82
Rocky	Ovate	6.59	Round	10.96	7.35	72.60	27.84	46.30

Table 6.--*Seasonal variation in titratable acid number (TAN)*[1] *in different parts of* Zizyphus nummularia *from sandy and rocky habitats (Nanda 1969)*

Plant parts	Monsoon		Winter		Summer	
	Sandy	Rocky	Sandy	Rocky	Sandy	Rocky
Root	8.21	27.64	3.1	5.26	17.71	6.23
Young stem	36.40	51.38	16.05	21.46	52.03	24.59
Mature stem	19.08	31.00	4.42	9.25	10.27	9.95
Young leaf	69.51	43.82	20.46	34.9	79.88	61.75
Mature leaf	38.51	29.25	14.49	27.36	28.24	65.55
Total	141.81	163.10	58.43	97.42	188.24	168.07

[1]TAN is expressed as the number of ml. of decinormal NaOH required to neutralize the acid contained in boiled residue originating from 100 g. of fresh tissue.

Economic use

Shrub species in the arid and semiarid regions are few, and the vegetation is rather sparse and open; but plants have been put to diverse uses by local populations. In the following tabulation the shrub species of this region are grouped according to their uses:

Use	*Plant species*	*Parts used*	*Disease*
Medicine	*Adhatoda vasica*	Leaves	Cough
	Aloe vera	Pulp	Gout
	Barleria prionitis	Bark	Fever
	Calotropis procera	Leaves	Cough
		Latex	Boils
	Capparis spinarum	Berry	Fever
	Carissa congesta	Berry	Fever
	C. opaca	Roots	Simla disease of cattle
		Roots	Decoction as insect repellent
	Ephedra foliata	Roots	Cardiac ailments
	Flacourtia indica	Bark	Eczema
	Glycyrrhiza sp.	Stem	Throat ailments
	Hemidesmis indicus	Root	Snake bite and venereal disease
	Holerrhena antidysantrica	Stem and root	Dysentery
	Mimosa rubicaulis	Bark	Insect repellent
	Rhus mysurensis	Stem	Fever
	Securinega virosa	Leaves and stem	Earache and headache
	Woodfordia fruiticosa	Roots	Rheumatic pain
	Zizyphus nummularia	Fruit	Stomach disorders
	Z. xylopyros	Bark	Astringent

Use	*Plant species*
Fencing and shelter beds	*Aerva tomentosa* *Calligonum polygonoides* *Crotalaria burhia* *Euphorbia caducifolia* *Leptadenia pyrotechnica* *Zizyphus nummularia*
Fibers for mats, rope, and baskets	*Agave sisalana* *Calotropis procera* *Calotropis gigantea* *Leptadenia pyrotechnica* *Tephrosia falciformis* *Vitex negundo*
Fuel	*Capparis decidua* *Carissa spinarum* *Euphorbia caducifolia* *Zizyphus nummularia*
Food and fodder	*Capparis aphylla* (fruit) *Carrisa congesta* (fruit) *Euphorbia neriifolia* *Opuntia dillenii* *Zizyphus nummularia*

	Shrub	*Use*
Miscellaneous	*Adhatoda vasica*	Wood for gunpowder, charcoal
	Cassia auriculata	Bark for tanning
	Holarrhena antidysentrica	Wood for carving
	Mimosa rubicaulis	Wood for tent pegs
	Securinega virosa	Wood for small agricultural implements

Indicator value

It is well known that plant cover indicates the geologic and hydrogeologic status of the habitat. Phreatophytes serve as very good indicators of the presence of water. Since contact of roots with ground water is essential for survival of the plant, the presence of plants indicates presence of a water table. Further, shrub growth may indicate presence of minerals. Ancient Hindu literature is full of such details, and Rishis such as Saraswat, Manu, Garga, and Varahmitra established a dozen ground-water indicators. Interestingly, all of the indicator plant species are shrubs (Gupta 1965).

Recently, studies at Central Arid Zone Research Institute at Jodhpur (Chatterji and Gupta 1969) have established relations between shrub species, depth of water table, and mineral content (figs. 3 and 4).

Occurrence of *Euphorbia caducifolia* on the volcanic hills and of *Acacia senegal-Anogeissus pendula* on granite loess indicate ground water to a depth of 10 m. with salt content of 1,500-10,000 p.p.m.; also, ground water to depths of 12-24 m. with total salt content of 500-1,000 p.p.m. A community of *Salvadora oleoides-Prosopis cineraria* on older alluvium has somewhat mineralized ground water (500-1,500 p.p.m.) at moderate depths (6-20 m.). *Acacia nilotica*, *P. cineraria*, and *Salvadora oleoides*,

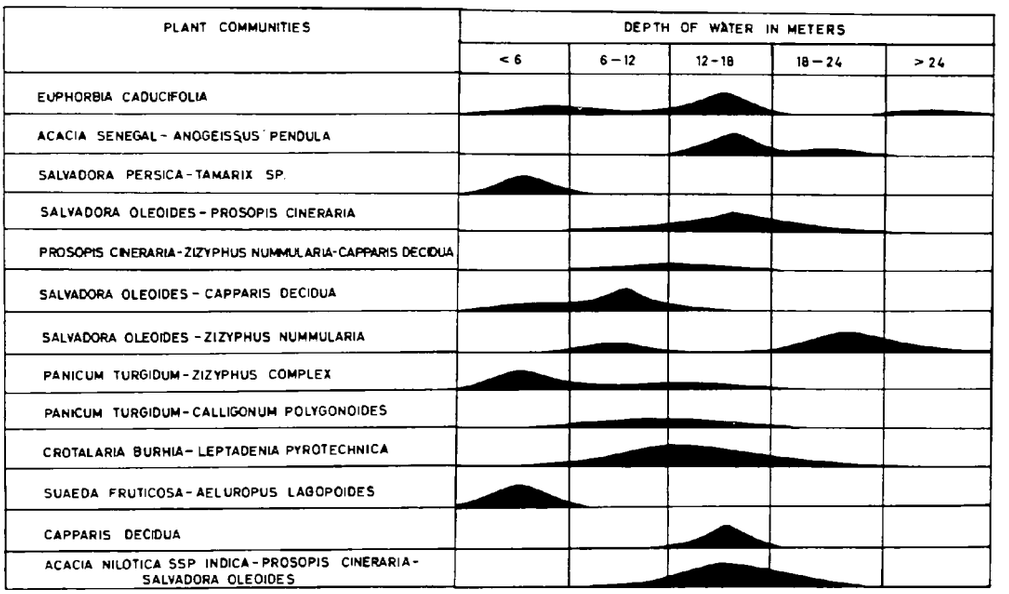


Figure 3.--Plant communities and depth of ground water.

though on older alluvium, unlike the plant community just mentioned indicate low mineralization (180-1,000 p.p.m.) at moderate depth (12-20 m.). *Prosopis cineraria*, *Zizyphus nummularia*, *Capparis decidua*, *Salvadora oleoides-Capparis decidua*, and *S. oleoides* and *Zizyphus nummularia*, indicate high salinity (5,000-10,000 p.p.m.) at depths of 9-15 m., 24 m., 3-9 m., and 18-24 m. in depth, respectively. Also, *Panicum turgidum-Zizyphus* complex (top of dunes) indicates 7,000-10,000 p.p.m. salinity at 3-9 m. depth, and *P. turgidum-Calligonum polygonoides* have established 9-15 m. depth and 1,500-3,000 p.p.m. salinity. On the other hand, a *Crotalaria burhia-Leptadenia pyrotechnica* community indicates 180-5,000 p.p.m. salinity at 9-15 m. depth. *Capparis decidua*, however, shows 300-9,000 p.p.m. salinity at 12-18 m. depth. Even so, a *Sueda fruticosa-Aeleuropus lagopoides* stand has a very high salinity (more than 12,000 p.p.m.) at 6 m. depth. Thus, it may be seen that the associations of shrubs are adapted to some lithologies that are characterized by definite hydrogeologic properties. These may therefore give an insight to the hydrogeologic condition of the area.

In addition to serving as an indicator of depth to water and of salinity, the presence of a given shrub species may also indicate the nature of hard pan, a clayey layer that is common and is still in the process of formation in arid zones of the

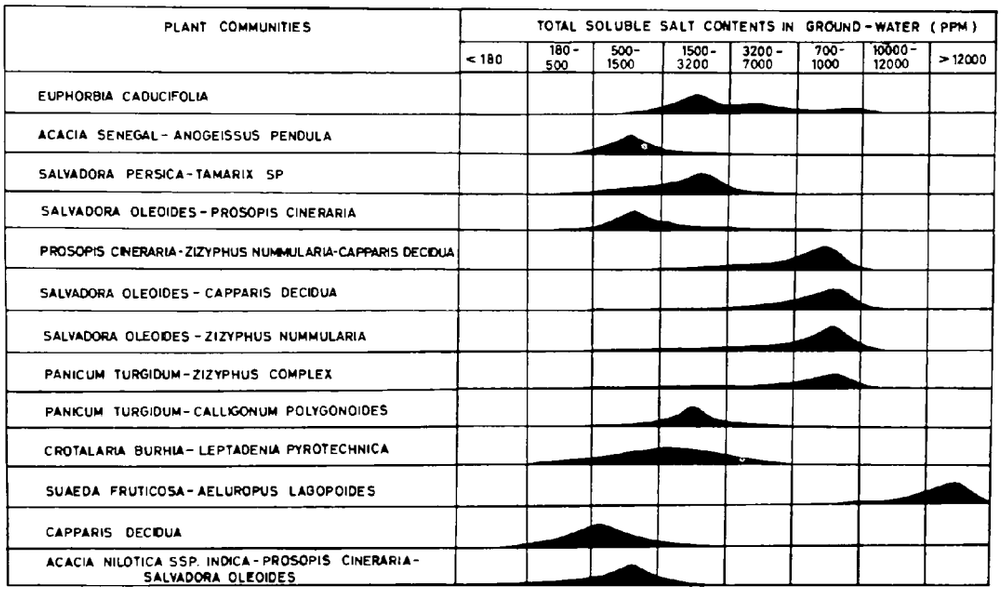


Figure 4.--Plant communities and total soluble salt content in ground water.

after CHATTERJI & GUPTA 1969

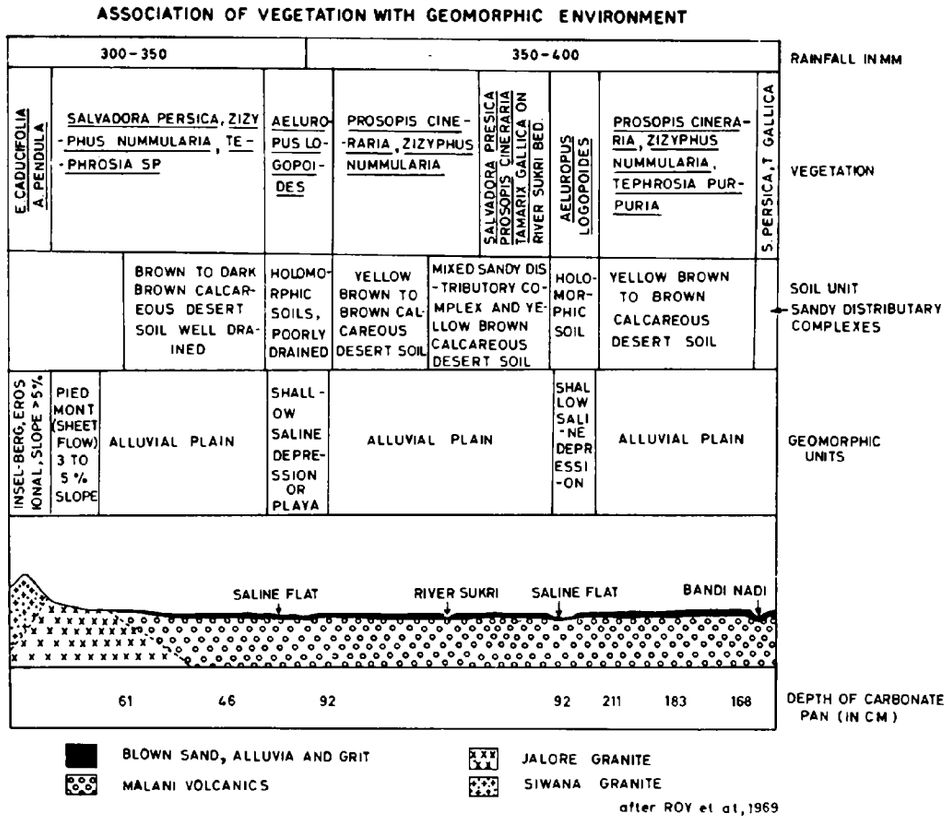


Figure 5.--Association of vegetation with geomorphic environment.

Indian subcontinent. The sparse, open vegetation found on calcareous and saline soils, and the mineralized ground water of this region are mainly due to the development of the carbonate pan. Shrubs and trees emerge only through the faults in this pan or in the grooves filled with alluvia or sand, and it is through these cracks that roots can penetrate. On the other hand, shrubs and grasses grow in areas which have shallow soils, and here the available water is more saline. This has been partially proved by plantation trials where plants did not succeed unless grooves were made into the pan (Kaul and Ganguli 1964). The Kankar Zone, or pan, is thin in piedmont sloping plains but the thickness increases considerably in the alluvial plain and depressions (fig. 5). Also, pan formation is not encountered in the inselberg zone. This varying depth of the pan is reflected by the distribution of shrubs and other plants. Thus, depending upon the nature of the pan, the vegetation changes (see fig. 5). *Euphorbia caducifolia* occurs on inselberg zones; whereas, depending upon the pan, *Salvadora persica-Zizyphus nummalaria* associations (168-180 cm. depth) are distributed in different regions. Where the pan is near the surface and draining is poor, grasses abound (Roy and others 1969). Thus, the distribution of shrubs in an arid or semiarid region is an indirect indicator of the geomorphic environment.

Conclusions

This Symposium was designed to bring together some main concepts of shrub biology, plus the known techniques of shrub utilization; then to identify the areas where knowledge is insufficient to make better use of the potential that shrubs can provide for man. With this objective in mind, some information regarding shrubs of the Indian subcontinent has been summarized in this paper. However, available data on shrub biology are admittedly meager; therefore, intensified research in this subject is needed.

Bhimaya and Ahuja (1969), while classifying the grasslands of arid and semiarid regions, associated shrubs like *Lycium europaeum, Tephrosea purpurea, Mimosa hamata,* and other thorny representatives with "Very Poor" type grasslands. They indicated that such types occur on eroded soils and produce 200 kg./ha. of dry matter per year (only

of grasses). It is not established whether the low productivity of this type is because of habitat or is due to shrubs. However, the point that must be appreciated is that shrubs flourish where grasses fail. Hence, the prime need is to identify several useful dominant shrubs and to study their biology so that their potentialities will become known as have those of *Zizyphus nummularia* (Nanda 1967, 1969). The next step should be to improve these shrubs genetically for better production or yield. Along with this, an important step should be to introduce new shrub species that would help increase the productivity of the land as well as lessen the grazing stress on the existing shrub species. Knowledge of seasonal behavior and composition of plant parts is necessary for effective pasture management. Such information would not only help in the maintenance of shrub species but would also be valuable in maintaining the health of cattle.

Another important problem that needs investigation because data are not now available is the effect of shrubs on the microenvironment. Such studies have been done for some tree species (Singh and Lal 1969). *Acacia nilotica* and *Prosopis specigera* considerably modify the microenvironment around them even though they occur together. Similar results have been shown (Dakshini 1968) wherein the soil mosaic is formed because of the activity of plant species occurring within very short distances of each other. On the basis of this dynamic aspect of plant and habitat association Dakshini (1970) suggested use of the "Soil Catena" concept in the classification of arid-zone soils of north India.

Attention should be given to the ethnobotany of shrub lands. This is important because most arid regions are dominated by nomadic tribes whose livelihood depends mostly on shrubs (by making fibers, baskets, ropes, mats, etc.) and other plants. A detailed study of the useful wildland shrubs would give further insight to shrub uses and their behavior and maintenance, thus indirectly encouraging small cottage industries, that would uplift the socioeconomic status of these nomadic tribes.

Arid areas generally have the reputation of inadequate or limited natural resources of soils, landscape, water, and vegetation. In the present context of shrub biology a reappraisal of resources through integrated survey is required.

Australia

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In this paper the term "shrub" includes naturally occurring woody perennial plants whether they have shrub forms or are small trees. Larger trees harvested mainly for the production of wood (lumber) are excluded.

As might be expected, the greatest emphasis is placed on edible species, since edibility is the characteristic that makes wildland shrubs most useful to man. However, some consideration is given to woody plants that have other desirable characteristics such as capacity to provide shade or shelter, to retard or prevent soil erosion, or to create microenvironmental conditions favorable to the growth of other useful species. Woody plants that are toxic or that reduce the productivity of grazing land by competition with other fodder plants are sometimes mentioned but are not discussed in detail.

Situation, physiography, climate, soils, and land use

Situation and area

Continental Australia covers about 7,690,000 sq. km. (2,968,000 sq. mi.). The island continent covers 7,617,000 sq. km. (2,941,000 sq. mi.); it lies between lat. 10°41' S. and 39°10' S. and long. 113°08' E. and 153°39' E. Tasmania, south of the mainland, has an area of about 68,300 sq. km. (26,380 sq. mi.), and several much smaller islands total about 4,700 sq. km. (1,814 sq. mi.).

Physiography

Australia is the world's flattest continent. Average elevation is less than 300 m. (1,000 ft.) above sea level; three-quarters of the land lies between 200 and 300 m. (600-1,000 ft.) above sea level, and only about 5 percent of the continent is higher than 600 m. (2,000 ft.). The highest peak, Mt. Kosciusko, in southeastern New South Wales, has an altitude of only 2,250 m. (7,305 ft.) and there are no permanent snowfields.

The continent comprises three major structural compartments:

1. A stable Western Platform extending from the Indian Ocean eastward for about 2,000 km. (1,200 mi.) into the Northern Territory and central Australia, with an average elevation of about 300 m. (1,000 ft.);

2. a Central Basin of gently warped, relatively young sedimentary rocks sloping upward from below sea level at Lake Eyre in northern South Australia eastwards for a distance of about 1,000 km. (600 mi.); and

3. the Eastern Uplands, a region of ancient orogeny rejuvenated with differential uplift during Tertiary and later time but showing subdued crestal contours even on the higher mountains.

Climate

According to Fitzpatrick and Nix (1970), Australia has the unenviable distinction of being the world's most extensively arid continent. Less than 7 percent of its land receives average annual rainfall exceeding 1,000 mm. (40 in.), and 70 percent receives less than 500 mm. (20 in.). In Central and Western Australia, more than 2,600,000 sq. km. (1,000,000 sq. mi.), about one-third of the total land surface of the continent, receives less than 250 mm. (10 in.) per year; in many places the average annual rainfall is only about half that amount. The Great Sandy Desert, Gibson Desert, Victoria Desert, and Simpson Desert occupy about 20 percent of the entire continent.

Mean annual rainfalls in excess of 1,500 mm. (60 in.) are recorded only in the extreme north of Cape York Peninsula and in localized areas along the eastern seaboard, the southeastern highlands and the west coast of Tasmania.

Incidence of rainfall ranges from predominantly summer in northern regions to predominantly winter in the south. Across the northern third of the continent is a well-defined wet summer and dry winter; in southwest Western Australia and southern South Australia there is a clearly marked wet winter and dry summer. In some of the wetter areas in the southeastern part of the continent, in western Tasmania, and in a broad ill-defined zone of transition from summer to winter rainfall through New South Wales, South Australia, and Western Australia, seasonal distribution of rainfall is fairly uniform; but in the less humid areas rainfall is erratic and unreliable. Inland areas and most of Western Australia are semiarid to arid, with erratic distribution of rainfall; the winter component increases and the summer component decreases in amount and reliability from north to south.

Soils

Hubble (1970) described 47 soil groups in Australia and indicated that most of the major groups have equivalents in some other part of the world. He pointed out that the soils of Australia present several features that give the continent a distinctive character. The most striking of these features are:

1. A generally low nutrient content with widespread and severe deficiencies of phosphorus and nitrogen and varied deficiencies of several trace elements;

2. poor physical condition of many surface soils, notably a tendency to surface sealing and to set hard on drying;

3. large areas of soils having strongly weathered or differentiated profiles, particularly those having strong texture contrast;

4. conspicuous lack of correlation of the distribution of many soils with climate, especially in the subhumid and drier regions;

5. presence of many soils that exhibit a curious pattern of mounds and hollows (gilgais or melon holes).

Land use

More than 37 percent of the Australian continent is not used for regular agricultural or pastoral production. Most of this unused or partly used land is either arid or very infertile or both, and apparently is incapable of producing more. In the better watered areas the only unused land is either reserved for National Parks or other purposes, or is occupied by cities or industrial enterprises, or is too wet, too rough, or too infertile to produce crops or livestock. Forests managed for timber (lumber) production occupy a little more than 2 percent of the continent.

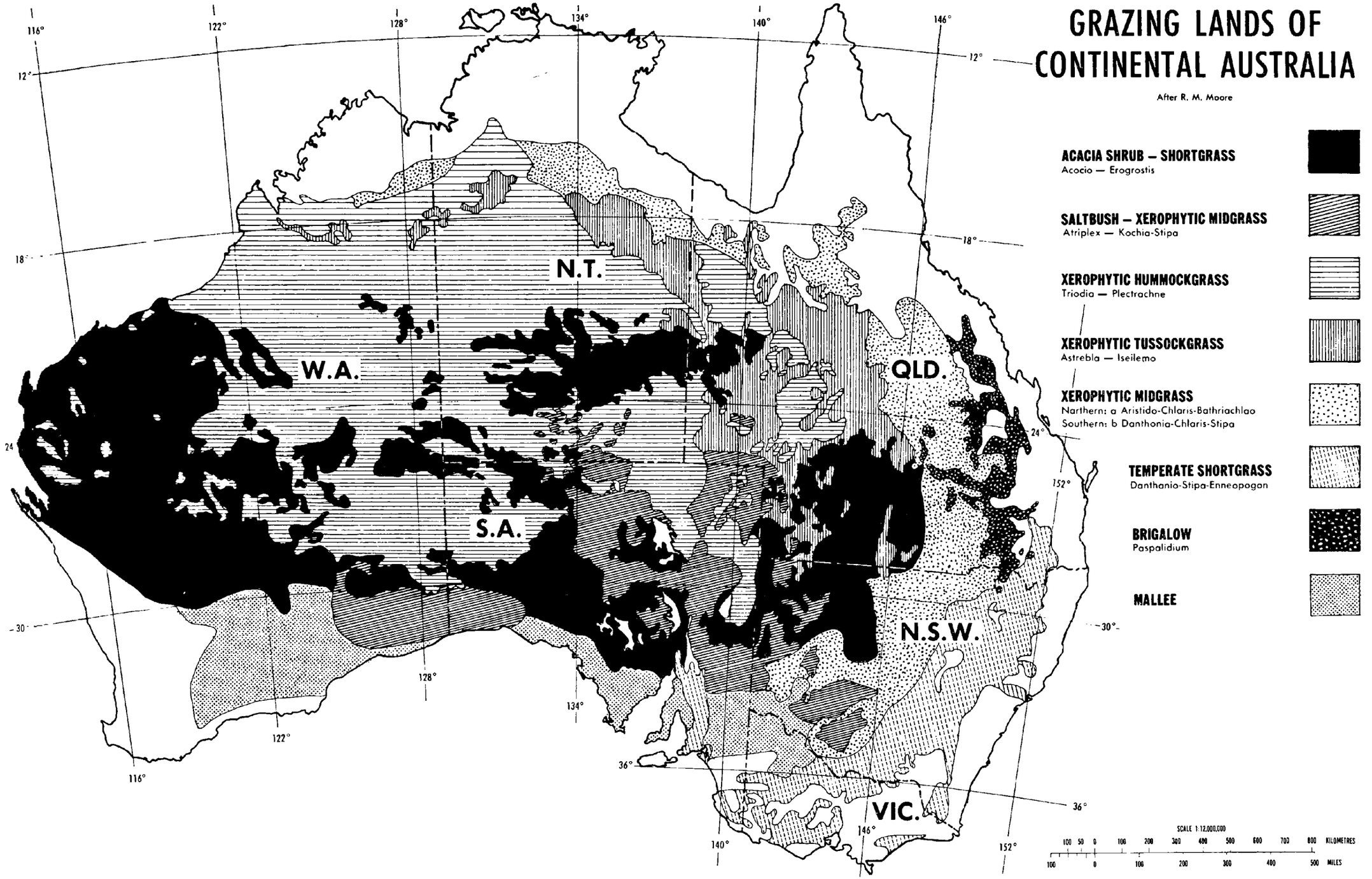
GRAZING LANDS OF CONTINENTAL AUSTRALIA
After R. M. Moore
ACACIA SHRUB – SHORTGRASS
Acocio — Erogrostis
SALTBUSH – XEROPHYTIC MIDGRASS
Atriplex — Kochia-Stipa
XEROPHYTIC HUMMOCKGRASS
Triodia — Plectrachne
XEROPHYTIC TUSSOCKGRASS
Astrebla — Iseilemo
XEROPHYTIC MIDGRASS
Northern: a Aristido-Chloris-Bathriachloa
Southern: b Danthonia-Chloris-Stipa
TEMPERATE SHORTGRASS
Danthonia-Stipa-Enneapogon
BRIGALOW
Paspalidium
MALLEE
N.T.
W.A.
QLD.
S.A.
N.S.W.
VIC.
SCALE 1:12,000,000
KILOMETRES
MILES

Figure 1

About 60 percent of the continent is used for agricultural or pastoral production. The total area of sown pasture amounts to about 3 percent of the whole land areas and agricultural crops use about another 2 percent; so about 55 percent of the continent is "grazing land" as defined by Moore (1970).

Most of this grazing land is fenced and occupied permanently under either leasehold or freehold tenure. There is little open range and no nomadism in the sense that owners or herders of livestock move seasonally to new pastures.

In the more arid regions, severe drought sometimes imposes a form of seminomadism: landholders may move their livestock away from drought-affected areas rather than allow them to die on the property or embark upon the uncertain and often uneconomic enterprise of hand-feeding imported fodder to the animals. At the end of the drought, properties are restocked either by returning the original animals or by buying fresh ones.

Wildland shrubs have greatest importance on these grazing lands, mostly as useful species but sometimes as invaders of and competitors with the plants upon which animals depend for survival or production, or both. Distribution of the grazing lands is shown in figure 1.

Edible shrubs and trees

It is less than 200 years since European grazing animals were introduced to Australia and only about 150 years since they were first taken to the semiarid and arid regions of the continent. During this comparatively short time, landholders have amassed considerable empirical knowledge about the palatability and approximate fodder value of the native plants, including the shrubs and small trees that are frequently known in local idiom as "topfeed" or "scrub."

Botanists, stock inspectors, and others associated with pastoral production have recorded much of this information and from time to time have published accounts of the distribution and behavior of particular shrubby species or plant communities or of the edible trees and shrubs of particular regions.

Review of Literature

The first real attempts to summarize existing information about the edible shrubs and trees of Australia were included in the worldwide Imperial Agricultural Bureaux Joint Publication No. 10, *Use and Misuse of Shrubs and Trees as Fodder* (1947). In that volume, edible shrubs and trees of each Australian State were discussed separately by different authors, each with a different background and method of approach to his subject. This piecemeal treatment produced no clear picture of the resources, utilization, or potential of shrubs as fodder for the continent as a whole.

In a privately published booklet, Corbet (1957) reviewed information about the fodder trees of Australia. He briefly discussed about 50 native and six introduced species and strongly urged landholders to preserve and manage these plants as valuable components of their native pastures.

Chippendale and Jephcott (1960) produced an Extension booklet in which they included notes on palatability, fodder value, and proximate chemical analyses for 60 different species of shrubs and trees used as "topfeed" by cattle in the Northern Territory.

In *The Trees of New South Wales*, Anderson (1957) included notes on the usefulness or otherwise for fodder of many of the species he described, but he devoted no chapter specifically to edible species. Stannard and Condon (1968) discussed in some detail 18 species of woody plants considered to be important as fodder in the grazing lands of western New South Wales.

A booklet by Everist (1969) published notes on 97 native and 16 introduced woody plants used as fodder for sheep or cattle in Queensland. It includes a table of proximate fodder analyses for 54 of the native and 11 of the introduced species and some notes on the digestibility of three of the most important native species. In a book now in press, R. M. Moore has discussed the role of trees and shrubs as fodder for sheep in Australia.

Occurrence and community distribution

A review of the literature, supplemented by personal observation and experience, indicates that more than 200 species of woody plants in Australia have been reported as being eaten by livestock. However, this number includes many whose value must be considered somewhat doubtful, mainly because their distribution is highly localized or because they are generally unpalatable and are eaten only occasionally. In fact, the really widespread and valuable species do not number more than about 40, but many others are important locally. It is inevitable that wildland shrubs and trees should have greatest value to livestock in semiarid and moderately arid regions and have least value in humid regions where sown pastures and crops can be grown to provide virtually all the forage that livestock require.

Moore has noted that edible shrubs and trees grow throughout the arid and semiarid zones of Australia as components of shrublands, shrub-steppe and shrub and low woodlands. More specifically, he stated that the grazing lands in which these plants contribute most to the feeding of sheep are the Xerophytic Midgrass, Acacia Shrub-Shortgrass, Saltbush-Xerophytic Midgrass, and the Brigalow communities. To this I would add that in many of the areas mapped as Xerophytic Tussockgrass and Xerophytic Hummockgrass, the contribution of shrubs and trees to the survival of livestock is often significant, particularly in dry years, and that even in parts of the Tropical Tallgrass zone, certain woody species, notably a *Planchonella*, a *Dolichandrone*, a *Dendrolobium*, and a *Wrightia* are regularly used as fodder for cattle. In Moore's latest work (in press) the map of the principal area of edible native trees and shrubs shows seven different communities.

It is convenient to discuss communities containing edible shrubs and trees under five main headings:

Shrub-Steppe Communities

These occupy an estimated 223,000 sq. km. (87,000 sq. mi.) in semiarid and arid regions of southern Australia where rain falls mainly in winter and the soils are pedocalcic and somewhat saline. Most of these communities are within the zone marked as Saltbush-Xerophytic Midgrass in figure 1. The principal perennial components are saltbushes (*Atriplex* spp.) and bluebushes (*Kochia* spp.), all much-branched shrubs from less than 1 m. to more than 2 m. high, readily accessible to livestock and with space between them to permit the growth of some perennial and many annual grasses and forbs.

Layered Woodland Communities

These have an upper story of palatable trees or tall shrubs, sometimes above the reach of grazing animals, together with lower layers of scattered palatable and unpalatable shrubs and a ground layer of grasses or forbs or both.

The best examples are the various mulga (*Acacia aneura*) communities. These occur on pedalferic soils extending in a discontinuous belt from the Western Australian coast across the southern edge of the central deserts to western New South Wales and southwestern Queensland, with another area of substantial size north of the central arid area in the Northern Territory. Mulga is the most important edible woody species in Australia, mainly because it is palatable, abundant, and widespread in regions of low

rainfall on land where the surface soils can grow grasses and forbs of only poor to moderate quality. Mulga communities, together with mixed mulga-hummockgrass communities and mulga-midgrass communities, occupy about 1,500,000 sq. km. (570,000 sq. mi.), or about 20 percent of the total area of the continent.

In the more arid western parts of the zone understory shrubs, mainly *Acacia*, *Rhagodia*, and *Eremophila* spp. are the chief sources of forage for livestock, and ground vegetation is mostly sparse and ephemeral. In central Australia and the more arid parts of western Queensland and New South Wales, mulga usually grows in groves that receive runoff water from the sparsely vegetated intergrove areas. These groves frequently include other edible shrubs and have a discontinuous ground layer of annual and perennial grasses and forbs. In the eastern part of the zone, mulga grows in tree form to a height of about 8 m. (25 ft.) and is often so dense (800-5,000 stems per ha.) that it prevents or seriously limits the growth of ground vegetation, unless thinned out by deliberate clearing or by major drought. On the eastern margin, the mulga woodland passes gradually into mixed woodland and mulga remains as an understory component on the western edges of the woodland communities dominated by *Eucalyptus*.

Mixed Woodland Communities

These have an upper layer of unpalatable trees (mainly *Eucalyptus* or *Acacia* spp.) and scattered palatable shrubs or trees, either in the upper layer or as an understory. They usually have a ground cover of perennial and annual grasses and forbs, the vigor and density of which depend largely on the density of the upper tree layer. Gidgee (*Acacia cambagei*) and brigalow (*A. harpophylla*) often grow in dense "scrubs" on heavy clay soils. Poplar box (*Eucalyptus populnea*) forms more open woodlands on the lighter sandy soils. The importance of woody plants as fodder in these communities depends on situation, soil, and methods of treatment and management.

These various communities occupy a total area of about 544,00 sq. km. (210,000 sq. mi.) and are widespread in the eastern half of the continent, mainly between the humid areas and the more arid regions.

Low Woodland Communities

In these, the dominant trees are low but unpalatable, and the ground layer of annual or perennial forbs, grasses, or both, includes some scattered palatable shrubs, particularly such Chenopods as *Atriplex*, *Kochia*, and *Bassia*. The mallee country is the best example. This occupies about 150,000 sq. km. (51,000 sq. mi.) across southern Australia between saltbush steppe and the more humid regions. It is characterized by the dominance of various species of *Eucalyptus* of peculiar habit, i.e., a short trunk at or below ground level, and several slender, spreading, or obliquely ascending branches up to about 3 to 5 m. (10 to 15 ft.) high.

Grassland Communities

The perennial tussock grasslands on the heavy clay soils of the tropical and subtropical regions, the temperate shortgrass communities of southern New South Wales, and the hummock grasslands of the sandy and stony soils of arid regions in the interior are often treeless or almost so. However, in many places edible shrubs or trees are present in sufficient numbers to be significant as food or shade for livestock. These are either scattered throughout the grassland or, more often, aggregated in clumps in particular habitats within the grassland communities.

The total area occupied by tussock grasslands has been estimated at about 2,500,000 sq. km. (980,000 sq. mi.). It is difficult to determine what percentage of these grasslands contains important numbers of shrubs, but it would be at least one-third of the total.

In Queensland and the Northern Territory, *Chenopodium auricomum* (northern bluebush) often forms conspicuous communities of low, palatable shrubs in low-lying areas. In the temperate shortgrass of southern New South Wales, the species of *Atriplex* and *Kochia* characteristic of adjacent shrub-steppe communities may be present, and some authors have stated that the shortgrass is a subclimax community induced by sheep grazing. In the hummock grasslands and in most other tussock grasslands, edible shrubs occur mainly as scattered individuals or small clumps of species identical with those found in adjacent woodland communities.

Utilization

In shrub-steppe communities and some of the more arid parts of the mulga belt, woody plants are principal perennial components of the vegetative cover and are therefore the basic resource upon which rests the long-term productivity of the plant community. The drought resistance of the Chenopods that are the dominant components of the temperate shrub-steppe communities is apparently due chiefly to special physiological characteristics of the plants rather than to structural adaptation. The palatable shrubs in both these types of community are very sensitive to excessive grazing pressure.

In other communities where perennial grasses and forbs are plentiful, woody plants are useful to grazing animals in two ways:

1. *As a source of protein* to supplement the high-fiber, moderate to high-energy diet provided by grasses during the dry part of "normal" seasons; and

2. *as reserves of fodder* sufficient to maintain at least some of the animals during drought after the ground vegetation has died or become nonproductive.

Usefulness of shrubs and trees as forage for livestock depends on three characteristics: *palatability, availability,* and *digestibility.*

Palatability

The most important characteristic is palatability. No matter how abundant or how nutritious a plant may be, it has no value as fodder unless animals eat it.

However, in some situations, great palatability can be a distinct disadvantage--not to an animal but to the plant itself. Excessive grazing pressure on a palatable species can lead to its destruction and disappearance from the original community. This has happened to some perennial saltbushes *(Atriplex)* and bluebushes *(Kochia)* in the shrub-steppes of southern Australia and to some of the palatable species of *Rhagodia* and *Eremophila* in the mulga country of the Murchison-Gascoyne country in arid Western Australia.

In the shrub-steppes, the more palatable shrubby species are sometimes replaced by less palatable and less productive shrubs, particularly in the more arid parts of the zone. In the more humid areas adjoining the temperate shortgrass communities, the original perennial shrubs may be replaced by perennial shortgrasses (e.g., *Danthonia*) and it has been suggested that these subclimax shortgrass communities are more productive for sheep than the original saltbush communities.

Poor management of shrubby communities leading to replacement by inferior species can have serious effects on long-term productivity and, even if livestock are totally excluded, the period required for recovery may be 20 years or more.

There appears to be no reliable laboratory test for determining palatability and no absolute scale by which it may be measured. Palatability is an elusive characteristic, usually assessed subjectively by observation of animal behavior. It can be affected by

many variables, including the species, breed, and normal behavioral pattern of the animals under observation, and the species, genetic constitution, stage of growth and physiological condition of the plants, and such environmental factors as situation, soil, and seasonal conditions.

Nevertheless, some plant species appear to be consistently eaten by livestock, and these are the ones that have acquired a reputation as fodder plants. Mulga *(Acacia aneura)* is a good example. Other abundant species of *Acacia,* which have equal or better potential value as determined by chemical analysis, appear to be consistently unpalatable, at least to the majority of animals in most circumstances; these species have little importance as fodder. In eastern Australia, for example, such species as gidgee *(Acacia cambagei)* and brigalow *(A. harpophylla)* occupy very large areas of semi-arid land. Their potential value as fodder is at least as great as that of mulga; but because they are not eaten readily by sheep or cattle, it is more profitable to destroy these short trees and replace them with sown pastures or self-regenerating native grasses and forbs.

Availability

This is also an important characteristic. Unless a plant is available in reasonable quantity it can contribute little or nothing to the nutrition of livestock. Indeed, in some circumstances, the presence of a few highly palatable trees in a stand of moderately palatable ones may be prejudicial to the success of a drought-feeding operation. Merino sheep being fed on mulga alone, for example, must maintain a daily intake of at least 1.4 kg. (3 lb.) of dry matter per day in order to meet their energy requirements for survival. If their pattern of behavior is disturbed by the cutting of one or two trees of high palatability, they often waste so much time and energy moving to it and waiting for more that they fail to consume sufficient of the less palatable species, and their condition deteriorates rapidly.

Methods of Utilization

Shrubs and trees can be made available for livestock in several ways. Shrubs or trees too tall to be grazed need to be brought down within reach of grazing animals. A great deal of work has been done in Australia on methods for achieving this. The traditional method of handling almost all species has been to lop them with an ax. The recovery of individual plants depended upon their capacity to produce new buds from the cut stems.

During the last 20 years or so, labor to cut trees with an ax or chain saw has become increasingly difficult to obtain and machinery has become more readily available. Pushing with bulldozers, pulling with rope or chain, and pushing with front-end loaders are now the common methods of utilizing abundant species such as mulga for drought-feeding of sheep and, to a smaller extent, cattle. Mulga does not regenerate readily unless it is cut off or broken off in such manner that lateral branches are allowed to remain on the standing stump at a height above the reach of sheep. Large areas of mulga have been destroyed by indiscriminate mechanical clearing.

On the other hand, in the eastern parts of the mulga zone and in some of the less arid parts of the western Australian mulga zone, evidence indicates that the clearing of some of the trees increases the net productivity of the country by encouraging growth of grasses and forbs and by allowing the remaining trees to grow with greater vigor.

Regrowth and Regeneration

Many other Australian edible species regenerate rapidly after cutting, but in virtually all species it is necessary to make the cuts about head-high so that sheep cannot reach the new shoots and thus exhaust the tree's reserves by progressive

defoliation. Regeneration from seed, particularly of mulga, saltbushes and bluebushes, has been the subject of several studies. Field observations on mulga in many parts of Australia indicate that germination is sporadic and that fairly well marked separate generations can be distinguished in most mulga communities.

Experiments in northwestern New South Wales (Preece 1971) showed that ripe seeds were produced only after a late summer flowering following rain, that hardseededness was common and that, on the assumption that the seed will soften naturally in a little over 6 months under field conditions, suitable conditions existed for germination of mulga near the study area once every 9 years.

Burbidge (1945, 1946) showed that seeds of saltbushes (*Atriplex*) and bluebushes (*Kochia*) in the shrub-steppe communities are not likely to remain viable for long under natural conditions. Matheson (1965) noted that *A. vesicaria* germinated only after a rain of at least 250 mm. (1 in.) or several falls of half that amount or more within a short time, and that several falls of rain in excess of 125 mm. (50 points) were needed within 2 months after germination for the young seedlings to survive.

Shrubs for other uses

Apart from studies of their use as fodder plants, the greatest attention paid to wildland shrubs has been as agents for control of soil erosion and as shelter for livestock. Retention of native woody plants for windbreaks and the planting of denuded areas have long been advocated in Australia but rarely acted upon by landholders.

A notable example of natural regeneration of native shrubs on a denuded area is afforded by a series of regeneration plots at Broken Hill, New South Wales, established by Albert Morris about 1930, primarily to demonstrate that the town could be protected from increasing duststorms and aridity and that the discomfort of the very harsh environment could be ameliorated by establishing vegetation on the denuded countryside. Morris' plots, combined with extensive plantings of native and introduced shrubs and trees, completely changed the face of the countryside in the immediate vicinity of the town and demonstrated that the harsh environment could be ameliorated.

Marshall recently (1970) completed studies on the possible role of shrubs in preventing wind erosion of susceptible soils in southern New South Wales. In wind-tunnel tests he showed that objects having a small ratio of diameter to height were most effective in reducing the velocity of surface wind and that the number of shrubs per unit area needed to reduce surface wind forces to negligible levels rises steeply as this ratio falls. He suggested that the optimum would be to have the ground incompletely covered by shrubs having a diameter-to-height ratio of 1:1 and spaced not further apart than seven times the height of the shrubs. In the field, wind erosion should be negligible in a community containing bladder saltbush (*Atriplex vesicaria*) 66 cm. (26 in.) high, spaced 178 cm. (70 in.) or less apart. Bluebush (*Kochia sedifolia*), with an average height twice that of bladder saltbush, should provide equal erosion protection at an average spacing of 305 cm. (120 in.) or less.

Shrubs trap surface soil where wind is actively eroding it, and many useful plants can germinate and become established in this windblown material. Whether shrubs are any more effective than perennial grasses in trapping windblown soil is not certain.

Other interesting local effects are the concentration of minerals or water or both under trees in arid and semiarid regions. Ebersohn and Lucas (1965) showed that in phosphate-deficient country in western Queensland, the amounts of phosphate and potassium in the surface soil under several woody species (mainly *Eucalyptus populnea*) were significantly greater than in the intertree zone. This mineral enrichment was considered to be an important factor in the establishment of cultivars of buffel grass (*Cenchrus ciliaris*) and to account for the presence of the native *Paspalidium globoideum* under trees but not elsewhere in the same plant communities.

Slatyer (1965) showed that in mulga groves in Central Australia more than 50 percent of the rainfall was channeled down the trunk into the soil at the very base of the tree.

Potential for wildland shrubs in Australia

It seems certain that the principal role of wildland shrubs in Australia will continue to be as fodder, shade, and shelter for livestock, mainly in arid and semiarid regions.

Work in progress at the Pasture Research Laboratory in Charleville, Queensland, the Arid Zone Research Institute, Alice Springs, and in the Western Australian mulga country will define quantitatively the value of mulga as fodder for sheep and cattle in various situations, will determine the optimum densities for mulga populations, and will provide guidance for proper management of mulga communities of different types and in different environments.

Studies by Leigh and others (1968) suggest that the original shrubby *Atriplex-Kochia* vegetation in the eastern parts of the shrub-steppe in southern New South Wales is less productive than the shortgrass that replaces it after continuous heavy grazing by sheep. The potential for shrubs in this zone is therefore in some doubt but, even so, many persons favor retention of a reserve of shrubs for fodder during the occasional drought. Marshall's work in the same area suggests that shrubs should be retained and perhaps encouraged to control wind erosion, irrespective of their value as drought fodder.

Work at Alice Springs and Adelaide (Maconochie 1968; Maconochie and Lange 1971) provides fundamental information on the patterns of growth in a number of arid-land woody species and, indeed, throws light on the mechanisms that produce the shrubby habit.

The future of shrubs as fodder plants in Australia might be profoundly affected by the future of the wool market. If the price of wool remains low, the pattern of land use in many regions might change radically, and the effects of such changes on the native shrubs cannot be forecast with any confidence, at least in most of the regions likely to be affected. Most of the information already available applies to the reaction of these ecosystems to grazing by merino sheep. Except in the Northern Territory, little information is available on the usefulness or otherwise of the major shrub species as fodder for cattle, or about the effects of the larger animals on the utilization or survival of the shrubs and trees themselves, or the possibility of invasion by unpalatable woody species. Digestibility trials, using cattle as test animals, are needed for almost all the native edible shrubs of Australia.

Planting

There seems to be little economic justification for the widespread planting of native trees or shrubs for fodder, at least in the semiarid and arid regions. Past experience and the few studies that have been made indicate that in the areas where they are most needed the climate is so harsh and rainfall is so unpredictable that mass plantings are unlikely to become established except with the expenditure of more money than is normally available for this purpose. However, in some situations inclusion of shrub species would be justified in sowing programs to reclaim eroded lands.

The potential of native shrubs for landscape planting appears to be considerable. There is a growing awareness of their peculiar character and their usefulness for creating special effects in landscape gardening. Furthermore, their hardiness makes many of them particularly suitable for stabilization and beautification of highway cuttings, fills, and similar situations. Considerable development in highway planting can be expected in nearly all areas where roadworks and industrialization are proceeding rapidly.

Africa -- the Mediterranean region

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This paper discusses shrubs that grow in both arid and nonarid areas in the Mediterranean basin (southern Europe, the Near East, and North Africa) and in the "sahel" or sahelian belt of arid and semiarid countries south of the Sahara Desert (Mauritania, Senegal, Mali, Niger, Chad, and Sudan). Both these general areas are large and diverse in elevation, climate, soils, and plant communities. For convenience they may be classed into four ecological zones based generally on total average annual rainfall, thus: the nonarid Mediterranean zone, where annual rainfall averages 400 mm. or more; the arid Mediterranean zone, where rainfall averages between 100 and 400 mm.; the desert, where rain is less than 100 mm. annually; and the tropical arid zone, where average annual rainfall ranges between 100 and 600 mm.

For this whole region the term "shrub" includes two essentially different types: tall shrubs, 0.5 to 3.0 m. high, and low shrubs, 0.20 to 0.50 m. high. This admittedly arbitrary classification corresponds roughly to Raunkiaer's (1905) worldwide classification of biological types. The tall shrubs, with several stems, correspond to his nanophanerophytes, and the low small shrubs to his chamaephytes. Many of the tall shrubs would grow to tree size under natural undisturbed conditions, but they hardly ever do so because of overgrazing and other current mismanagement practices.

All shrubs native to these regions are useful. Many species are browsed and often constitute the only feed reserve during recurrent periods of drought; they thus enable survival of millions of animals that otherwise would perish (table 1). Other uses of shrubs in this region and the genera used for them include: charcoal (*Quercus, Olea*); distillation (*Rosmarinus*); human food (*Capparis, Opuntia, Arbutus*); medicines (*Acacia, Cassia*); tanning (*Quercus, Acacia, Rhus*); dyes (*Tamarix, Rhus, Lawsonia*); ornamental plantings (*Nerium, Tamarix, Atriplex, Rosmarinus, Buxus*); and tools (*Olea*). Roots of *Erica arborea* are used for manufacturing "briar" pipes for smokers. All these shrubs are occasionally used for fuel, and many are important in controlling wind erosion and protecting catchment basins in the arid and semiarid zones.

Shrubs make it possible to establish settled farming in areas where nomadism would otherwise be the only "agriculture." Shrubs and trees are often the only possible feed reserves on huge grazing areas; they enable livestock to survive long dry seasons. They are essential to livestock production in developing nations in the Mediterranean region and in the Sahelian arid belt south of the Sahara because of their ability to extract water from deep layers of the substratum. For example, *Atriplex halimus* can get water from depths of 10 m., and living roots of *Zizyphus lotus* have been found at 60 m. in southern Morocco. This is why shrubs can remain productive during the dry season in many areas where common perennial fodder plants hardly survive. The role of shrubs and trees as fodder increases with the irregularity of the distribution of rainfall and the length of the dry season.

Table 1.--*Populations of cattle, sheep, and goats in Europe, Asia, and Africa in 1966-1968*[1]

Geographic area	Cattle	Sheep	Goats
		Thousands	
Europe			
Greece	1,100	7,900	3,800
Italy	9,500	8,200	1,100
Spain	4,000	18,000	2,600
Yugoslavia	6,000	10,000	20
Asia			
Iran	5,500	33,000	13,000
Iraq	1,500	11,000	1,800
Jordan	40	700	380
Lebanon	80	200	350
Saudi Arabia	150	3,900	3,000
Syria	500	5,900	740
Turkey	14,000	35,000	20,000
Africa			
Algeria	700	7,000	2,500
Chad	4,000	1,800	2,000
Libya	120	1,700	1,400
Mali	4,800	5,200	5,100
Mauritania	2,000	2,600	2,200
Morocco	700	14,000	7,800
Niger	4,000	2,500	5,800
Senegal	2,500	1,400	1,500
Sudan	11,200	11,000	8,400
Tunisia	600	3,400	500
U.A.R. (Egypt)	1,700	2,200	800
Totals	74,690	186,600	84,890

[1]Source: FAO Yearbook 1969.

Unfortunately, shrubs and trees are seriously mismanaged and are receding rapidly in the face of population pressures. Harm done during the last 30 years is probably much more serious than what was done during the course of the past few centuries where an equilibrium of man-livestock-vegetation had established itself. It is urgent that measures be devised and taken to protect, restore, and expand important species. Integrated research in plant physiology, ecology, genetics, nutrition, and animal feeding is urgently needed before many of these species are brought into standard agricultural routine.

Much is already known, mainly in the Mediterranean region, and the use of many species can now be extended. Experimental work carried on in Israel and Tunisia particularly shows the way for a new agricultural system for arid zones where exploitive agriculture has often become an economic failure and resulted in expansion of desert areas.

Mediterranean nonarid zone

Shrub vegetation resulting from depletion of various types of forests occupies extensive areas around the Mediterranean. We can assume that at least 65 percent of the land classified as "forest land" in these countries (at least in the Mediterranean zone) is shrubby vegetation called "garrigue," "maquis," or "matorral." Certainly not more than one-third of these so-called forest lands in the area may be considered as true productive timber forest. These estimates of area are disputable, but they suggest the importance of shrubs in the region. The area covered by this type of vegetation is large, but productivity is low.

Animal production probably represents 60 to 80 percent of the total economic production of the Mediterranean forest land, if we consider Morocco as a test case (Le Houérou 1971a).

In areas that receive heavy rainfall (800 to 1,000 mm.) the browse produced amounts to some 1,000 kg. of dry matter per hectare per year (Long and others 1967). This production is the same as that of the Californian "chaparral" and the Australian "mallee" (Specht 1967), under generally similar ecological conditions. Long and others (1967) showed that under proper management (brush cutting and fertilizing) this production may be increased by four to six times in certain areas; i.e., enough fodder to feed four to six sheep per hectare per year instead of only one. However, such an increase in amount and quality of fodder production would not be due to the shrubs alone but also to the grasses and legumes favored by a rational management.

Under lower rainfall conditions (550 to 600 mm.), Liacos and Moulopoulos (1967) found annual production of 400 to 800 kg. of dry browse per hectare per year in northern Greece; this means 25 kg. of meat on the hoof and 30 kg. of milk per hectare from goats.

These studies were made in France and Greece and both were concerned with "garrigue" shrublands of *Quercus coccifera*. In Morocco, a few surveys have shown that production averaged about 400 to 600 kg. of dry browse per hectare per year, and up to 1,000 to 1,200 kg./ha./year under the best current conditions (Le Houérou 1971a).

Types of shrublands

The Mediterranean shrublands result from forest degradation and can be classified into two main types; namely, open degraded forests and garrigue, maquis, and matorral shrublands.

The open degraded forests consist of rather scarce trees interspread in a generally thick shrub vegetation. The six principal open forest types are:

1. *Abies* degraded forests. These are at the higher altitudes and toward the limits of the Mediterranean and temperate climates. Species are *A. cephalonica* (in Greece), *A. cilicica*, *A. equi-trojani* (in Turkey), and *A. numidica* and *A. pinsapo* (in Algeria, Morocco, and Spain).

2. *Cedrus libanotica* degraded forests. These are in higher elevations (1,000 to 2,000 m.) of the Mediterranean region, in Turkey, Cyprus, Morocco, and Algeria.

3. Cork oak (*Quercus suber*) forests in Spain and North Africa.

4. Deciduous oak forests. *Q. cerris*, *Q. ithaburensis*, and *Q. boissieri* in the Near East, and *Q. faginea*, *Q. pubescens*, and *Q. pyrenaica* in North Africa and Spain.

5. Evergreen oak forests. *Q. calliprinos* in the Near East and *Cyrenaica*, and *Q. ilex* in North Africa, Spain, and France.

6. Pine degraded forests. *Pinus halepensis* in Europe and North Africa; *P. halepensis* and *P. brutia* in the Near East.

The three major types of shrubland are fairly distinct. The garrigue is a rather low open shrubland on very well drained and edaphically dry calcareous soil; it is often the result of degradation of a pine forest vegetation. The maquis is often a higher type of thick shrubland that generally occurs where there is more rainfall, better water balance, and somewhat less acid soils. It often replaces a cork oak forest vegetation, at least in the western Mediterranean area. The matorral somewhat combines the other two types and appears to be equivalent to the American chaparral.

Uses of shrubs

Shrubs are used as browse over this whole region. Other uses of shrubs and shrublands vary greatly from country to country, mostly according to the economic level of the rural populations. In the more advanced countries, shrublands are used increasingly for housing and recreation areas; in less advanced countries, where rural populations are at subsistence level, the people get most of their income from shrublands by making charcoal, distilling, cutting and selling firewood, clearing the land for cultivation, and raising goats and bees.

The principal species used for browsing are *Quercus coccifers* and *Q. ilex* in the central and western Mediterranean area, and their cousin *Q. calliprinos* in the Near East. These oaks are heavily browsed and have good feed value: about 0.6 Scandinavian Feed Unit and 70 g. of digestible proteins per kilogram of ovendried browse of *Q. coccifers* (Long and others 1964; Liacos and Moulopoulos 1967). They constitute the bulk of the fodder production of the garrigue.

Other principal browse species include *Arbutus unedo*, *A. andrachne*, *Calycotome villosa*, *C. rigida*, *Celtis australis*, *Ceratonia siliqua*, *Cistus libanotis*, *C. villosus*, *C. salvifolius*, *Citysus triflorus*, *Coronilla emeroides*, *C. glauca*, *C. juncea*, *C. minima*, *Colutea arborescens*, *Cupressus sempervirens*, *Erica arborea*, *E. multiflora*, *E. scoparia*, *Fraxinus oxophylla*, *F. ornus*, *F. xyloxanthoides*, *Globularia alypum*, *Juniperus excelsa*, *J. phoenicia*, *J. oxycedrus*, *J. procera*, *Medicago arborea*, *Olea europaea*, *O. chrysophylla*, *Ostrya carpinifolia*, *Phillyrea media*, *Pistacia khinjuk*, *P. palaestina*, *P. terebinthus*, *P. lentiscus*, *Rhamnus lycioides*, *R. palestinus*, *Rosmarinus officinalis*, *Styrax officinalis*, *Tetraclinis articulata*, *Ulmus campestris*, *Withania frutescens*, and others.

Mediterranean arid zone

The Mediterranean Arid Zone includes the arid shrublands of developing countries in North Africa and the Near East between the isohyets of 400 and 100 mm. The shrublands here can be classified as depleted forest, chamaephytic steppes, nanophanerophytic steppes, and halophytic crassulescent steppes.

Depleted forests

The depleted forest shrublands are on the hills and mountains of this zone. Shrub vegetation is similar to that of the garrigues of the nonarid Mediterranean zone, but the dominant species are not the same. The shrubs chiefly grazed are *Argyrolobium linneanum, Coronilla juncea, Juniperus phoenicia, Phillyrea media, Pistacia atlantica, P. lentiscus, Rhamnus lycioides, Rhus tripartitum, Rosmarinus officinalis,* and *R. tourneforti.*

Chamaephytic steppes

The chamaephytic steppes--some 10 to 20 million ha.--are covered by low (20 to 50 cm. high) shrub species; these plant communities cover large areas of the pediments and the plains. These shrublands result either from the depletion of gramineous steppes or from clearing land of aleppo pine and Phoenician juniper, followed by abandonment (Le Houérou 1968, 1969a). The main shrubland plant communities and areas where they commonly occur are:

Species	*Near East*	*North Africa*	*Spain*
Achillea fragrantissima	✓		
Anabasis aphylla	✓		
A. articulata	✓	✓	
A. oropediorum		✓	
Artemisia herba alba	✓	✓	✓
A. monosperma	✓		
A. campestris		✓	✓
Arthrophytum scoparium		✓	
A. schmittianum		✓	
Helianthemum lippii		✓	
Noaea mucronata	✓	✓	
Poterium spinosa	✓		
Rhantherium garcini	✓		
R. epapposum	✓		
R. suaveolens		✓	
Salsola rigida	✓	✓	
S. baryosma	✓		
S. vermiculata		✓	
Thymelaea hirsuta	✓	✓	

In their turn these shrublands are often depleted into fugacious, very short swards of *Poa sinaica, Carex stenophylla,* and *Stipa capensis* in the Near East; *Hordeum murinum, Cynodon dactylon,* and *Stipa retorta* in North Africa; or such unpalatable forbs as *Peganum harmala, Thapsia garganica, Cleome arabica, Euphorbia* spp., and others in both regions. The causes for this depletion are overgrazing, cultivation, and uprooting of the shrubs for firewood (1 kg. per person per day is an average need). Since the average shrub biomass of the shrub steppes is about 1,000 kg./ha. and the population of the arid lands of the Near East and North Africa is about 50 million persons, the acreage of shrub steppes destroyed yearly by uprooting would be estimated at about 3.5 million ha. Fortunately the actual net destruction is less than that because of some regeneration from natural reseeding during rainy years on areas where seed-producing plants remain. The problem of progressive depletion is extremely serious and contributes, with the addition of overgrazing and sporadic cultivation, to the encroachment of the desert over many tens of thousands of hectares every year (Le Houérou 1968, 1969a; Pearse 1970). The extent of this desertization is being experimentally surveyed in southern Tunisia (Floret 1971).

The yearly biomass of the arid chamaephytic steppes ranges between 300 and 4,000 kg./ha. of dry matter, with an average of 1,000 (Le Houérou 1969a, 1971; Rodin and others 1970; Floret 1971). Average fodder production is about 250 kg./ha./year of dry matter. A stocking rate of about 2 ha. per sheep-equivalent meets the figure of 250 kg./ha. of dry fodder and explains the low level of animals' productivity (0.4 lamb per ewe).

Nanophanerophytic steppes

The nanophanerophytic steppes are covered by rather sparse tall shrubs (0.5 to 3 m. high) interspersed between low shrubs and forbs and produce twice to three times more than the chamaephytic ones because they have deeper soils that have better water balance. They have counterpart types of vegetation in other arid zones; e.g., *Zizyphus lotus* plays the same role here as *Prosopis juliflora* (=*P. dulcis*) in the southern States of the United States, and northern Mexico. All these shrubs are used for both browse and firewood. *Retama retam* and *Atriplex halimus* are both very good browse. This type of vegetation grows on the deep soils and sand dunes and along the stream network on the terraces.

The main species on these nanophanerophytic steppes are *Acacia raddiana* (shrub or tree), *Atriplex halimus* (shrub or tree, southern Morocco only), *Calycotome rigida*, *C. villosa*, *Haloxylon persicum* (Near East), *Nitraria retusa*, *Pistacia atlantica* (shrub or tree), *Retama retam* (dunes), *Rhus pentaphyllum*, *R. tripartitum*, *Tamarix* spp., and *Zizyphus lotus*.

Halophytic steppes

Shrubs on the halophytic steppes are crassulescent species belonging mainly to the Chenopodiaceae family. They occupy the low parts of the andoreic basins on salty soils with or without a water table. This shrub vegetation is chiefly grazed by camels (dromedaries) and very often is uprooted for fuel. Production is about the same as that of the nanophanerophytic steppes, i.e., 2,000 to 3,000 kg. of dry matter per hectare per year.

Principal shrub species on these steppes are *Alhaghi maurorum*, *Arthrocnemum glaucum*, *Atriplex halimus*, *A. verrucifera*, *Halocnemum strobilaceum*, *Limoniastrum guyonianum*, *Salicornia arabica*, *Salsola tetrandra*, *Seidlizia rosmarinus*, *Suaeda fruticosa*, *S. mollis*, *S. palaestina*, *Traganum nudatum*, *Zygophyllum alba*, and *Z. dumosum*.

Desert shrub vegetation

Desert shrubs grow only in limited areas: along stream networks, in the cliffs of mountains and hills, and on dunes. These shrubs are used for firewood; nearly all are used for browse and many supply raw materials for drugs and medicines. In desert regions, the nomadic grazing herds subsist almost entirely on shrubs except during a few weeks after occasional rains. Major desert shrub species follow according to usual habitat.

Stream networks: *Acacia raddiana*, *Aerva javanica*, *Anabasis articulata*, *Artemisia judaica*, *A. tilhoana*, *Arthrophytum schmittianum*, *A. scoparium*, *Astragalus pseudotrigonus*, *Atriplex halimus*, *Belanites aegyptica*, *Calatropis procera*, *Cassia obovata*, *Crotalaria saharae*, *Leptadenia pyrotechnica*, *Maerua crassifolia*, *Pentzia monodiana*, *Pistacia atlantica*, *Pulicaria crispa*, *Retama retam*, *Salvadora persica*, *Tamarix* spp., *Traganum nudatum*, *Zilla spinosum*, *Zizyphus lotus*, and *Z. nummularia*.

Cliffs and hills: *Acacia mellifera*, *A. raddiana*, *A. seyal*, *Balanites aegyptica*, *Ficus ingens*, *Maerum crassifolia*, *Myrtus nivelli*, *Olea chrysophylla*, and *O. laperrini*.

Sands and dunes: *Calligonum arich, C. azel, C. comosum, Ephedra alata, Haloxylon persicum, Helianthemum brachypodium, Ochradenus baccatus,* and *Retama retam.*

Sahel zone[1]

The southern fringe of the Sahara, a tropical arid belt, is generally referred to as the "Sahel Zone" or "Sahel Belt." It covers some 400 to 600 million ha. between the 100 and 600 mm. isohyets. The climate is the dry tropical type. The two main seasons of the year are a dry season from mid-October to early July and a 2- to 3-month rainy season from July to mid-October. August and September are the two rainiest months, and precipitation increases from north to south. The "harmattan," a hot drying wind, blows during the dry season (chiefly in May and June) and raises the air temperature to 45°-50° C. These winds correspond to the sirocco of North Africa, which may blow from May to October.

The dominant human population is the Peul or Foulbé ethnos, often nomadic; they specialize in stock raising, mainly zebus. Soils usually are sandy, very poor, and swept by the winds during the dry season. The only permanent surface waters are in the Senegal and Niger rivers and Lake Chad.

These harsh environmental conditions do not allow a prosperous agriculture. The rain-fed crops can grow only during the short summer rainy season. Precipitation is generally low and varies greatly from year to year. During the rainy season, long intercalary dry periods may occur; they seriously reduce the yields of both crops and pastures.

Vegetation is steppic in the very border of the Sahara between the 100 and 200 mm. isohyets. Between the 200- and 600-mm. isohyets, vegetation is of the savanna type; trees are rather scarce and are interspersed with shrubs on a fairly continuous cover that is mainly annual grass. The term "bush-savanna," criticized by some geographers, is justified here by the universal presence of *Andropogon gayanus,* a tall perennial grass that likely is climax. However, this species is in evident regression caused by overgrazing and burning.

The main rain-fed crops are: (a) millet, or "small mil" (*Pennisetum galucum* = *P. typhoideum*), which is cultivated on sandy soils in the 200- to 400-mm. zone; (b) sorghum, or "large mil" (*Sorghum arundinaceum, S. vulgare,* many varieties), which is cultivated on the medium to heavy textured soils in the 400- to 800-mm. zone; (c) *Dolichos ungiculatus* or "niébé," a bean; and (d) *Colocynthis citrullus,* a watermelon, and "Guinean sorrel" (*Hibiscus sabdariffa*), the leaves of which are used as a vegetable food. All these are subsistence crops and are cultivated on only small areas.

The postflooding crops ("cultures de décrues") are cultivated in the flooded areas along the banks of the Senegal and Niger rivers. Major crops are millet, sorghum, and maize. A few vegetables also are raised in these areas; they include gombo (okra), *Hibiscus esculentus*; niébé, *Dolichos ungiculatus* and *Vigna sinensis*; kissi bean, *Phaseolus lunatus*, and pimientos, *Capsicum* spp.

The Sahelian zone actually is the main meat production area of Africa. It has some 30 million head of cattle, 25 million sheep, and 25 million goats (table 1). Cattle raising is by far the most profitable industry in this immense area. The stocking rate is about 10 ha. per head of cattle on a year-round basis.

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[1]This section has been prepared in collaboration with A. Naegelé, a specialist in the botany of this zone.

During the rainy season, there are no feeding problems. Water is available everywhere in temporary ponds for animal watering, and the supply of native grasses is more than sufficient to meet feed requirements and to permit fattening. Primary production from grasses averages about 2,000 kg. of dry matter per hectare per year. Consumption rate is about 60 percent (Gillet 1967; Naegelé 1971). All this changes during the dry season. Then the ponds are dry, wells are scarce, and the vegetation is dried up: grasses are merely straw on the stalk and have very mediocre feed value.

Large grazing areas are devastated every year by bushland fires ("feux de brousse") which cause high losses of animals. An average of 40 percent of the young cattle dies. Because of these fires the livestock can survive the dry season only because of the availability of shrubs and tree browse.

The acacias are such an important source of fodder that the Sahelian savanna is often called the "Mimosaceae savanna." More than a dozen species of acacia provide fodder, and more than 30 other species in 16 families supplement this. These shrubs and trees are extremely valuable; in fact, stock raising probably would not be possible without them in many locales. During the dry season they provide green feed (leaves, flowers, and fruits), often rich in proteins, vitamins, and valuable mineral elements. Wherever these shrubs and trees are absent, animals have only poor straw from native annual grasses. This very poor feed brings on avitaminosis and mineral deficiencies (chiefly phosphocalcic) that often cause a disease called "pica" that generates deadly toxemias.

These shrubs and trees are equally important to the pastoral population that lives in this southern belt of the Sahara. Besides providing feed for their animals, these plants also provide food for the people (fruits and leaves), plus materials for drugs and medicines, wood for fuel, and materials for housing, fencing, tools, and handicraft of varied sorts. Bark of some species is used in making rope. Unfortunately, these plants are not now sufficiently protected and consequently some of them are slowly disappearing. Man in the Sahelian savanna still acts as a predator; that is, he takes everything he can from Nature without doing anything to help maintain the production of valuable plants. It is urgent, therefore, to develop a rational policy for managing the ligneous resources of the Sahelian zone to prevent total desertization of the area. The present desertization of this zone is in no way due to any worsening of the climate; it is due solely to the destructive activity of man (Kassas 1970; Monod 1958; Dubief 1953; Aubreville 1949; Quezel 1958).

Shrubs as fodder crops for arid zones

In the arid zones of the Near East and North Africa, native ranges are being depleted rapidly; cultivation of cereal crops and fruit trees is expanding correspondingly. Irrigated fodder crops are rather scarce because water is expensive and irrigated areas necessarily are small. Consequently, livestock raising is becoming progressively more difficult and unproductive.

The remedy for this situation seems to be the growing of drought-resistant fodder crops, mostly shrubs and trees, under rain-fed conditions. Research and extension projects directed toward this problem have been carried on for many years in Israel and Tunisia; the result has been selection of a very few successful species, which, fortunately, are complementary both ecologically and dietetically. These are chiefly in the genera *Opuntia*, *Atriplex*, and *Acacia*.

Opuntia

Cacti have been known in the Mediterranean area for at least 400 years; they are reported to have been brought to Spain from America by Columbus' second expedition. From there they spread over all the Mediterranean region, probably during the conquests

of Philip II of Spain when the Moors were driven out. These species cover about 100,000 ha. in Sicily and even more in Tunisia; in the arid zone of Tunisia alone they cover at least 60,000 ha. Many experiments and farmers' experiences show that cacti can grow in areas receiving only 200 mm. of annual rainfall on deep sandy soils--on areas receiving only 120 to 150 mm. if supplementary runoff is available.

In Tunisia, plantations of the spineless *Opuntia ficus indica* are being increased by 3,000 to 5,000 ha. yearly. A rather elaborate technique for developing these plantations has been devised. It is designed to promote rapid growth of the cactus, use the limited supply of moisture effectively, and also keep wind erosion of the sandy soils to a minimum. In areas that receive only 150 to 250 mm. annual precipitation, the plantations have to be located in water channels and valleys; small earth dams are built to keep water from flowing away.

With this technique, yields are from 10 to 30 metric tons of green fodder per hectare in areas having light rainfall and up to 80 to 100 tons where rainfall amounts to 350-450 mm. In other words, in the drier areas the amount of feed produced is 800 to 2,400 Scandinavian Feed Units per hectare per year, and from 6,400 to 8,000 Units in wetter areas. This is enough feed reserve for eight to 24 sheep in the drier country, and 64 to 80 sheep elsewhere, considering the feed reserve should be 30 percent of the animals' total feed requirements.

Experiments and experience, though, have shown that this cactus feed is very unbalanced; it is particularly poor in protein and phosphorus. Sheep and cattle must receive 10 percent of the weight of cactus they consume as dry feed (straw, hay, or browse) in order to avoid diarrhea, but they may be fed for 6 to 10 weeks with cactus only without danger.

With the dry matter component in their diet, these animals can consume at least 10 percent of their body weight of cactus. That is, a sheep weighing 45 kg. can eat 4.5 kg. of cactus. This ensures maintenance of the animals over several months. For sustained production, supplementary protein-rich feed is needed, plus extra phosphorus. This supplementary protein may come from other cultivated shrubs such as *Atriplex* and *Acacia*.

The cacti now cultivated in North Africa have a difficult ecological problem. The strains of spineless *Opuntia ficus indica* do not withstand cold lower than -6° C., and that for only short periods. So these strains are automatically eliminated from areas where elevation is more than 800 to 1,000 m. Hence, we still have to find spineless varieties of cactus able to withstand temperatures of -12° to -15° C. and able to grow with only 150 to 200 mm. of rainfall, for these are the conditions met in large areas of the Algerian and Moroccan high plains. Unfortunately, in experiments to date, only spiny varieties of cactus have met these requirements for temperature and moisture.

Atriplex

The genus *Atriplex* includes several species very useful in arid zones. *A. nummularia*, *A. halimus*, *A. glauca*, and *A. vesicaria*, for example, can grow normally with only 150 to 200 mm. rainfall where soils are deep. Their frost resistance is high (-10° to -12° C.) and they can also withstand very heavy textured soils and very saline soils or waters, whereas cacti cannot grow under any of these conditions. Laboratory experiments have demonstrated that *A. halimus*, for instance, grows normally with as much as 30 g. per liter of sodium chloride in a nutritive solution (Zid 1970). Field experiments and farming trials have shown that good stands have been established on soils having electric conductivity of 40 to 50 millimhos in the extract of the saturated paste (Bouraoui 1969).

Other measurements have shown that either *A. nummularia* or *A. halimus* can produce 1,000 to 1,500 feed units per hectare with only 200 mm. of rainfall; this is eight to ten times more than a fairly good native pasture produces under the same conditions (Malet 1969; Ziani 1969). These species can survive (but without producing) with only 50 mm. of rainfall during 12 months (Francelet and Le Houérou 1971). Their nutritive value is very good; the digestible protein content is high and averages 12 percent on the dry matter; this is food value identical to that of alfalfa.

Some agronomists have questioned the palatability of *Atriplex* species. However, numerous experiments and farmers' experience show that the *Atriplex* are perfectly accepted during the summer and fall (July-November) when there is no green feed on the ranges. Cordier (1947) showed consumption of 3 to 4 kg. of leaves per sheep per day, and Sarson (1970) found that ewes weighing 45 kg. consumed about 2 kg. of *A. nummularia* or *A. halimus* per day after they became accustomed to this food over a 1-month period. Nevertheless, because of the rather high NaCl content of this fodder, its palatability may be impaired when drinking water also has a high salt content (Wilson 1964, 1966).

Experiments by Sarson (1970) in Tunisia have shown that fat-tail ewes weighing about 45 kg. could be kept in good condition with a slight weight increase when eating only *Atriplex, Opuntia,* and wheat straw. During his 2-month experiment, the intake of *Atriplex* and *Opuntia* increased progressively while straw intake decreased. At the start of this experiment, intakes for *Atriplex, Opuntia,* and straw were 0.430, 2.640, and 0.960 kg., respectively; by the end of the period they had increased to 2.091, 4.690, and 0.582 (Sarson 1970).

Cultivation is reasonably simple. Seedlings or cuttings are grown in a nursery for 3 to 6 months and then planted in the field early in the spring, preferably after rain, about 1 by 5 m. apart. Normally *Atriplex* spp. may be grazed when they reach 1.5 m. height, the second or third year, depending on local conditions. Shrubs are cut every 2 or 3 years. *A. nummularia* yields about 10,000 kg. of dry firewood per hectare over a 3-year period. Native stands of *A. halimus* yield about the same volume both in browse and wood (Ziani 1969; Rodin and others 1970; Le Houérou 1971c). *Atriplex* is now being cultivated as an arid land fodder crop, and several hundred hectares are being planted every year in Tunisia.

Significant differences have been observed within populations of several species; these have to do with salt resistance, drought resistance, salt content, leafiness, and palatability. This means that a wide field of research is open in genetics, physiology, ecophysiology, and nutrition.

Acacia

What has been said above about *Atriplex* is applicable to *Acacia.* Of several drought-resistant Australian species introduced into Tunisia a few years ago, three *(Acacia ligulata, A. salicina,* and *A. aneura)* have given very good results in areas where annual rainfall averages as low as 150 mm. Feeding trials with sheep have been satisfactorily conclusive, and a synergistic effect on sheep consumption was found between *Opuntia, Atriplex,* and *Acacia*: each of the three components of the diet increased significantly the intake of the other two. Yields of *Acacia* are comparable with those of *Opuntia* and *Atriplex*, and the field techniques are essentially the same as for *Atriplex.* The acacias, like the cactus but unlike the saltbush, need sandy nonsaline soils. Like both cactus and saltbush, though, they are being planted on several hundred additional hectares yearly in Tunisia (Le Houérou 1971b).

Other Species Cultivated as Fodder in the Mediterranean Region

Besides the species of *Opuntia, Atriplex,* and *Acacia* noted above, several other species of shrubs and trees have proved to be adaptable for culture for fodder in this

region. They are listed below in descending order of their minimum requirements for rainfall, shown as R.

Fraxinus oxyphylla. R>500 mm. This species of ash provides very good fodder, which is accepted by all herbivores.

Gleditsia triacanthos, common honeylocust. R>400 mm. This species is desirably frost resistant, and its leaves and pods are good fodder. Palatability varies considerably among strains.

Morus alba, white mulberry. R>350 mm. This shrub is grazed by all ruminants and provides fodder comparable to alfalfa.

Vitis spp. (*V. vinifera,* European grape; *V. rupestris,* sand grape; *V. berlandieri,* winter grape). R>300 mm. All three species provide good fodder that is accepted by all ruminants. Because of their prostrate habit, the American *Vitis* spp. are especially useful as fodder shrubs as well as for soil protection.

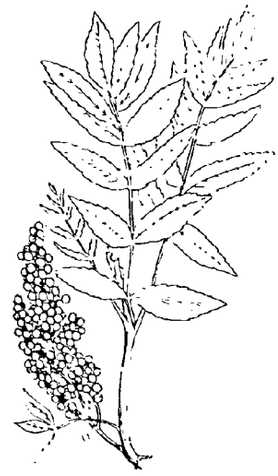
Eleagnus angustifolia. R>300 mm. This shrub is widely used in the Near East but to a lesser extent in North Africa. It is very frost resistant and provides good fodder that is accepted by all herbivores.

Ceratonia siliqua, carob, or St. Johnswood. R>200 mm. This is a well known native and cultivated fodder tree. It is drought resistant but is sensitive to frost.

Olea europaea f. *oleaster,* wild common olive. R>150 mm. This tree is grazed heavily because it provides good fodder for cattle, sheep, goats, and dromedaries.

Prosopis juliflora, mesquite. R>150 mm. The leaves and pods of both shrub and tree forms provide good fodder, but palatability varies among strains. The species is frost sensitive.

Chenopodium auricomum, goosefoot. This Australian "blue bush" was introduced only a few years ago; its moisture requirements have not yet been definitely determined. All ruminants like its foliage, which has high protein content. Since it appears to be very drought resistant, it is a promising species for propagation in the Mediterranean arid zone.



Asia

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Natural features of arid areas of Asia

Arid areas of Asia cover an extensive territory within the boundaries of temperate, tropical, and subtropical zones. They are located within the territory of such countries as the U.S.S.R., the Chinese People's Republic, India, Pakistan, Afghanistan, Iran, Irak, Turkey, the nations of the Near East, and the Arabian Peninsula. Some of these countries lie entirely within arid areas.

According to calculations by P. Meigs, the area of arid lands within the boundaries of Asia is approximately 16.5 million sq. km. Extra-arid deserts occupy more than 1 million sq. km., arid deserts cover about 8 million sq. km., and dry deserts and savannas occupy about 7.5 million sq. km. Arid areas comprise nearly 40 percent of the surface within the temperate zone, about 33 percent in the subtropical zone, and 26 percent of the tropical zone (fig. 1).

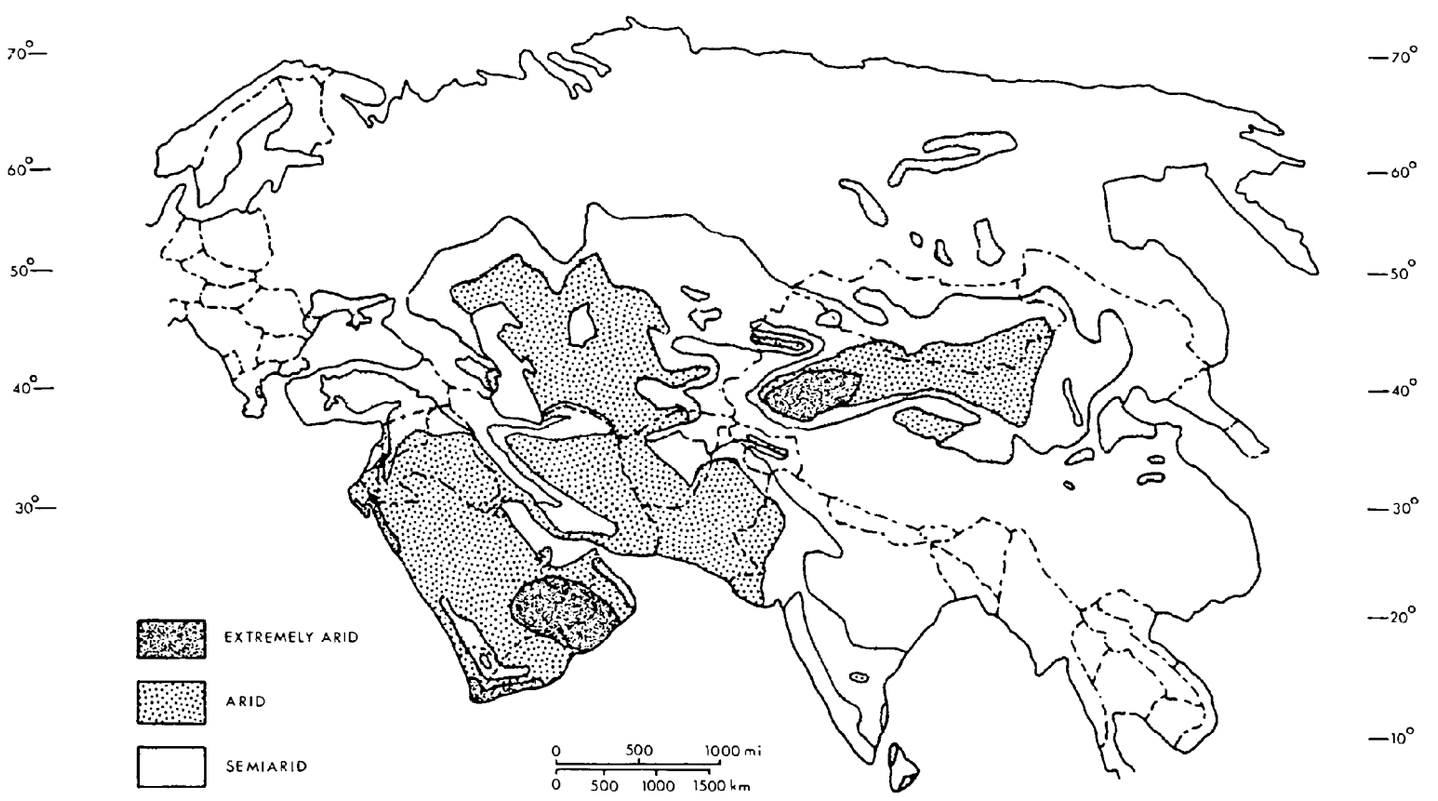

Figure 1.--Arid regions of Asia.

Table 1.--*Climate of deserts and semideserts of Asia*

Station	Height above sea level	Mean air temperature			Annual precipitation
		January	July	Annual	
	M.	- - - - - °C.- - - - -			*Mm.*
Guryev	-22	-10.4	25.4	7.8	164
Aral Sea	57	-13.5	26.3	6.8	103
Repetek	186	0.8	32.3	16.6	107
Ansi	1,122	- 9.8	26.3	9.6	42
Charchan	966	- 9.7	25.5	9.9	9
Saynshand	911	-18.1	23.3	3.8	107
Isfahan	1,773	2.5	27.9	15.4	117
Girishk	945	8.5	33.5	20.7	168
Tadmor	420	6.9	29.2	15.8	93
Maskat	29	17.7	33.5	25.6	100
Ar-Riyad	600	14.1	33.4	24.3	75
Bikaner	245	14.7	33.3	26.4	292
Khanpur	99	13.3	35.8	25.7	164
Multan	128	13.6	34.6	25.3	182

Arid areas are found in five geotectonic regions: Central Asia, Middle Asia,[1] Iranian upland, Arabian Peninsula, and the Indus depression, sometimes called the Thar desert. Most of these areas are situated in the interior of the continent; the deserts of the Arabian Peninsula are an exception because they extend to the seashores.

The deserts and semideserts occupy surfaces from differing geologic origins; ancient alluvial plains, sheet structural plains, mountains, and uplands. Ancient alluvial plains are mainly covered by sandy deserts such as Lower Kara Kum, Takla-makan, Sary-Tshik Otrau, the greater part of the Alashan desert, Kuzupchi sands in Ordos, and others. In Tsaidam under such conditions, Solonchak deserts predominate.

Pebbly-sandy, detrital-gypsified, and occasionally sandy deserts (Ust-Urt, Zaunguz plateau, Kyzyl Kum, and part of the Dzungarian desert, of Tsaidam, Alashan, Ordos and of the Arabian peninsula) are confined to Tertiary and Cretaceous structural plains. At the same time there are considerable massifs of rock-waste deserts formed in place of peneplained mountainous uplifts (Betpakdala, low hills of Kazakhstan, Peishan, Iranian upland). Sandy and pebbly-sandy deserts are prevalent.

Climate of the arid areas of Asia is classed as semiarid, arid, and extra-arid in temperate, subtropical, and tropical zones. The temperature regime is rather severe. Average monthly air temperature in the tropical and subtropical zones in the hottest months exceeds 35° C., and the absolute maximum temperature rises to 50° C. (table 1). Winters are warm, and average monthly air temperatures in January are above zero. In deserts in the temperate zone, summers are cooler (25° to 30° C.) but winters are severe; average monthly winter temperature is about -12° C.

[1]Soviet geographers apply the term "Middle Asia" to the territory of Soviet Middle Asia alone, and refer to the territory east of Tien Shan and Pamirs as "Central Asia."

Besides air temperature, moisture conditions are important in the rhythm of vegetative life in arid areas. Precipitation is especially important. Three types of precipitation regimes prevail in the arid areas of Asia: the eastern Mediterranean, Chinese, and Indian monsoonal. The regime determines the different correlations of heat and moisture in different seasons and deserts. Thus, a winter-spring maximum precipitation is typical for the Mediterranean region and the south of Central Asia, and it causes rapid growth of vegetation during the moist spring period. Summer is hot and dry in these territories; consequently, most plants are considerably depressed in their growth and development; some become biologically dormant.

The deserts of eastern and southeastern Asia have a summer maximum of precipitation that is associated with the eastern Chinese and Indian monsoons; the outburst of vegetation there occurs in the second half of the summer. Spring is rainless and dry, and in the deserts of Central Asia it is also cold. Therefore, the period of depression in the development of vegetation in these areas includes spring and the first part of summer. Such variety of edaphic and climatic conditions has caused considerable ecological differentiation in shrub vegetation.

Features of the geographic distribution of shrubs

Soviet botanists and ecologists consider undershrubs to be plants of comparatively low height (up to 6 m.), characterized by intense growth of several axes resulting from reduction of the mother stem.

Shoots on shrubs dry up more markedly than those on trees. Skeleton axes of shrubs in desert and semidesert areas of Central Asia develop early in their ontogeny. Their lifespan nearly equals that of the mother axis. All branches of the first order and some of those of the second die off and are replaced. The length of yearling shoots is less than half the length of perennial branches.

Floras of individual arid sections of Asia have many common or closely similar species even though the sections are separated and isolated by formidable mountain uplifts. Thus, the Thar Desert in the depression of the Indus River is separated on the west from the arid areas of the Mediterranean regions and from arid Asia by the Iranian upland and high Hindu Kush Mountains; it is separated from the deserts of Central Asia by the Himalayas. In spite of this, the floras of the Thar Desert and those of deserts in arid areas of western Asia--even up to North Africa--have much in common.

Zochary (1963) declared that the exchange of floras between the delta and the valley of the Indus, southern Iran, and the Arabian Peninsula could have gone on along the coasts of the Arabian Sea, Persian Gulf, and the Gulf of Oman. Among these plants can be included the halophytic shrub *Lycium* and psammophytes of the seashore sand ridges--species in the genera *Prosopis, Acacia, Cassia, Calotropis, Procera,* and others.

The second route of the migration of flora was across the Iranian upland and the Hindu Kush. This route connected the floras of the Near East and Central Asia with the floras of the arid areas of India. Species of the genera *Calligonum* and *Haloxylon* can be regarded as representatives of this migration.

The structural complexity of the surface of the extensive Iranian upland territory and the variety of edaphic conditions determined the isolation of the areas of some plant species that had migrated across the Iranian upland and the Hindu Kush. There are some specific features in the distribution of shrubs of the arid zone of Asia. The territory where these shrubs grow is regarded as one of the Holarctic and Paleotropic botanical-geographical areas.

Lavrenko (1962, 1970), following Eig (1930), marked out two botanico-geographical areas in the arid zones of Eurasia and North Africa--the Sahara-Gobi Desert

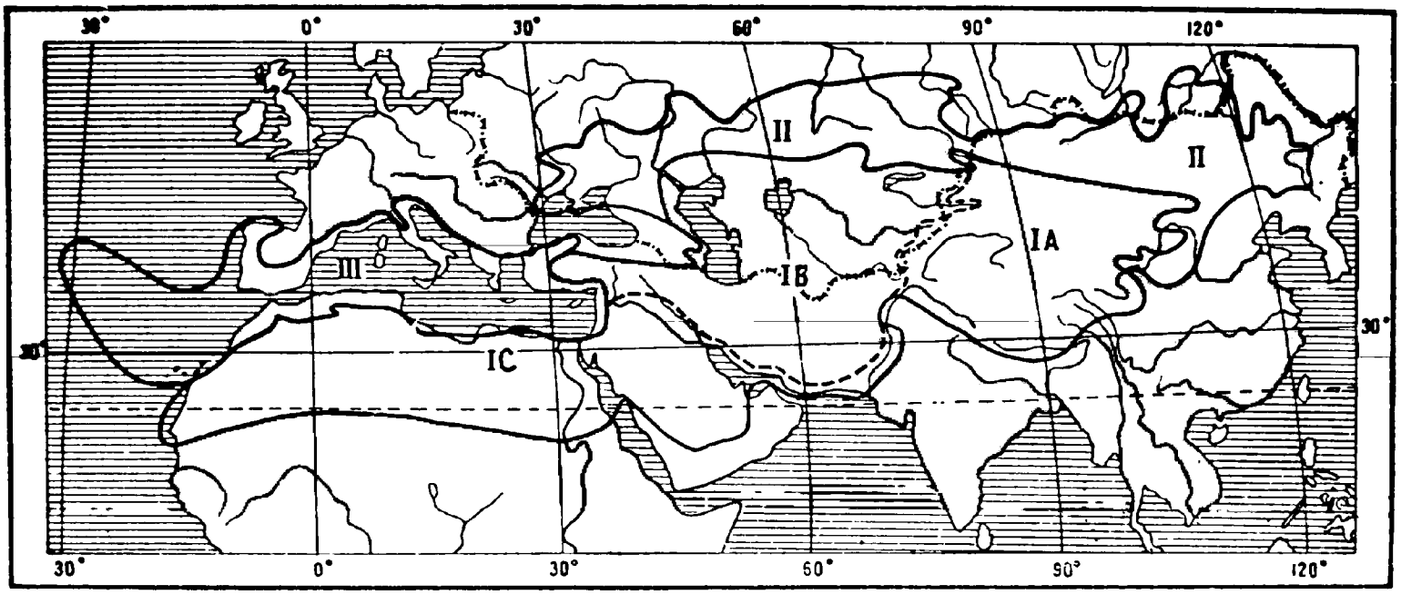

Figure 2.--Phytogeographical division of arid zones of Asia and North Africa (by Lavrenko). I, Sahara-Gobi desert region. IA, Central Asiatic subregion. IB, Irano-Turanian subregion. IC, Sahara-Sindian subregion. II, Eurasiatic steppe region. III, Mediterranean evergreen region.

area and the Eurasian area. The former is divided into Central-Asian, Irano-Turanian, and Sahara-Sind subareas and the latter into the European-Kazakhstan and Central-Asian subareas (fig. 2).

The areas occupied by Turanian and Central-Asiatic shrub species illustrate features of the geographic distribution of shrubs. Some cosmopolitan shrubs occupy an area lying within several natural zones. These are halophilous shrubs of the genera *Haloxylon, Salsola, Halostachys, Kalidium, Halocnemum,* and others. Preliminary calculations indicate that their number is several hundred. The three families that include the most shrub species are the Chenopodiaceae (*Salsola, Haloxylon, Kalidium, Anabasis,* and others), Polygonaceae (*Calligonum, Atraphaxis,* and others), and Leguminosae (*Acacia, Astragalus, Hedysarum,* and others). The variety of species is not great and they are but weakly differentiated ecologically and are mainly xero-mesophytes: *Caragana, Spiraea, Cerasus, Amygdalus,* and *Spiraeanthus.*

In a desert zone where annual precipitation exceeds 100 mm., the role of shrubs notably increases. Thus, in sandy, rocky, and saline deserts, shrubs predominate in a number of areas and determine the aspect of plant growth. This gives the Soviet geobotanists a reason for calling these deserts "shrub deserts."

The ecological variety of desert shrub species is rich. According to the edaphic conditions these shrubs can be regarded as halophytes, petrophytes, psammophytes, and gypsophytes. There is little variety in shrub species in the extra-arid areas of Central Asia and Arabian Peninsula because of severe environmental conditions. Sandy soils in semideserts are occupied by the species of local vegetation--pine forests in deserts of the U.S.S.R., and Acacia savanna in Western India (Rajasthan).

In some arid areas of Asia shrubs form climax communities, notably in sandy deserts. In deserts of Central Asia, geobotanists distinguish the following shrub formations: *Haloxyloneta aphylli, H. persici, Ammodendreta, Eremospartoneta, Tamariceta aestivale, Salsoleta psammoarboreta, S. albae, S. arbusculaeformae, Calligoneta fruticosa, Lycieta deserta, Nitrarieta deserta, Halostachyeta, Kalidieta, Halocnemeta, Ephedreta deserta, Anabaseta aphylli,* and others (Nikitin 1966).

The thickets of shrubs in sandy deserts result from the more favorable water regime of loose sandy soils. Usually sands easily absorb water and store it at some depth. Because of this there is little direct evaporation and all moisture is utilized by the plants. Some shrub deserts exist because of ground water.

Thickets of halophytes can be seen all over the arid zone. Their moisture comes from close-lying ground water.

Species-edificators[2] in the sandy deserts of Asia are *Haloxylon persicum, Haphyllum, Halimodendron, Salsola richteri, Calligonum* spp., *Ephedra strobilacea,* and *E. lomatolepis.* They grow either as unmixed thickets or together with other shrubs and occupy extensive areas. For instance, the community of *Haloxylon persicum* in the Kara Kum occupies a band about 100 to 200 km. wide from the frontier of Afghanistan to the Caspian Sea, The low shrubs *Halocnemum strobilaceum, Seidlitzia* spp., *Kalidium* spp., *Halostachys,* and others are the edificators of saline deserts.

Ecology of shrubs

Investigation of the relations between plant organisms and their environment, as well as research into the modes of plant adaptation to the dry, hot climate of deserts, has great scientific and practical interest.

Intense solar radiation and associated high temperatures, dryness of the air, and shortage of soil moisture are the most important climatic factors of the deserts to which plants must adapt. To exist under such conditions, plants need thermoregulating mechanisms for ensuring their generally constant temperature and water regime.

There are three major adaptation groups:

1. *Formative forms,* which include morphological and anatomical features of plants (fig. 3), which control chiefly the water balance and salt regime through aphylly, microphylly, a well developed root system, developed epidermis protective properties, availability of water-storage tissue, salt-excreting glands, and so on.

2. *Physiological forms,* which include peculiarities of photosynthesis, respiration, transpiration, resistance of protoplast to high temperatures, high content of salt in cell sap, and synthesis of water-retaining substances (ethereal and fatty oils, butyl substances, alkaloids, and so on).

3. *Peculiarities of rhythm and rate of development,* displayed in vigorous vitality during periods of favorable combination of heat and moisture, and retirement into dormant state with the advent of high temperatures and droughts.

If environmental conditions deteriorate, the protective reaction of plants appears not in a single adaptation feature but in a system of features functioning as a complex.

The most varied forms of plant adaptation are related to the main limiting factor--deficiency of humidity in the air and of moisture in the soil. The adaptation is achieved by a xeromorphic appearance and structure of the plants as well as through peculiarities of their physiological processes.

Studies of ecological peculiarities of desert plants (eremophytes) all over the world show that plants' manner of adaptation is similar whether in widely separated deserts or merely in different systematic groups within a single desert.

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[2]In Russian ecological publications this word means "environment-forming plants."

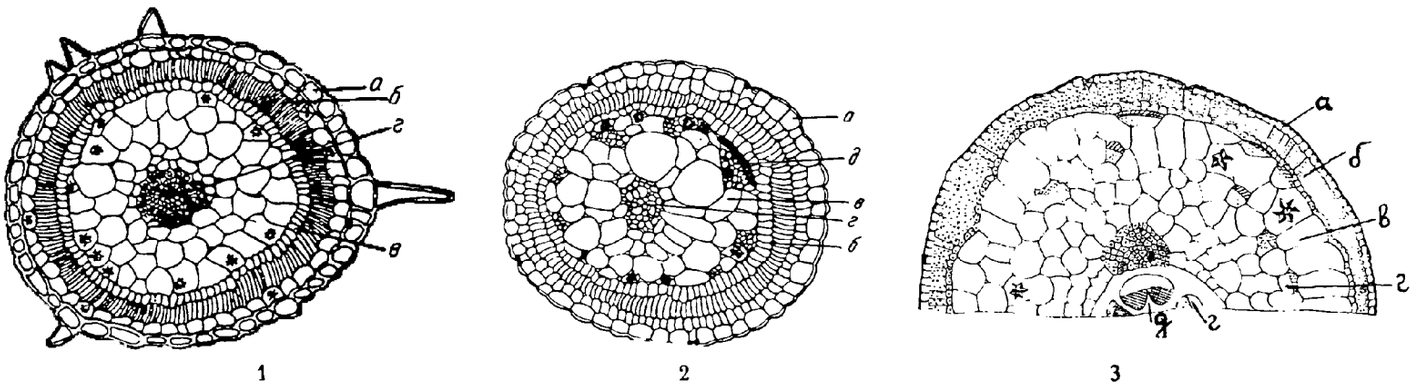


Figure 3.--Anatomy of leaves and aphyllous shoots of desert shrubs. Transverse sections: 1, Leaf of Salsola richteri*; 2, assimilative shoot of* Calligonum caput-medusae*; 3, assimilative shoot of* Haloxylon aphyllum.

By virtue of some differences in environmental conditions but mainly by virtue of genetic features, two basic ecological types of plants have developed--succulents and sclerophytes. In addition to the previously mentioned common features, the succulents are characterized by abundance of large-skeletal thin-wall living tissues, which accumulate water; the reduction of water-conducting and reinforcing tissues; low osmotic pressure, low transpiration rate, slow growth, and high heat resistance. The sclerophytes are characterized by predominance of thick-wall ligneous tissues, small cells, high osmotic pressure, vigorous transpiration and respiration, and comparatively rapid growth. The high heat resistance of plants of this ecological type is due mostly to the high rate of transpiration. Besides these two types, there are halophytes, which are widespread on saline soils; they too are characterized by reduced evaporating surface, high tissue density, and high osmotic pressure. However, most halophytes have no structural protective devices in their epidermis against evaporation, and some of them have salt-excreting devices.

In deserts of the tropical zone, which have warm winters, all three of these ecological types of plants can be found--succulents, sclerophytes, and halophytes. In deserts of the temperate zone the sclerophytes and halophytes prevail. Existence of typical succulents is impossible in these cooler deserts because of subzero winter temperatures. However, some species, such as *Calligonum*--in assimilative twigs, and *Zygophyllum*--in leaves, have large-celled tissues that accumulate water, but these organs are shed at the beginning of autumn.

In spite of a considerable difference in floral composition, ecological features of desert plants in different continents have much in common; this is manifested in the convergence of adaptation forms revealed in the morphological and physiological features of plants, as well as in the rate and rhythm of their development, conforming to their habitat. A classic example of convergence in the plant world is the unusual resemblance between the succulent representatives of such systematically remote families as Euphorbiaceae and Cactaceae.

The similarity of sclerophyte plants belonging to different genetic groups is displayed by the presence of virgate leafless green shoots (aphylly). This feature is characteristic of some representatives of the Leguminosae--*Eremospartum flaccidum* and *Spartium junceum;* the Rosacea--*Amygdalus scoparia;* the Polygonaceae--*Calligonum;* the Chenopodiaceae--*Haloxylon, Haolenemum, Kalidium, Arthrophytum, Hammada,* and others. Thus, similar physical and geographical conditions give rise to plants similar in biology, rhythm of development, character of morphological and physiological features, and good adaptation to the severe conditions of deserts.

Edaphic conditions are of great, sometimes decisive, importance for the ecology of plants. Depending on these conditions, the shrubs of arid areas can be divided into five groups.

1. Halophyte shrubs growing on soils with sulphate-chloride salinity and close-lying saline ground water--in Solonchak depressions and littoral Solonchaks. These are aphyllous or microphyllous plants, with thick segmented twigs and usually succulent leaves. The cell sap is saturated with water-soluble salts--sulphates and chlorides. Sometimes the salt content comprises up to 45 percent of absolute dry weight of the leaves. The abundance of water-soluble salts increases the osmotic pressure of cell sap and retards transpiration. In some halophytes osmotic pressure reaches 200 atm. (*Haloxylon aphyllum*, 88 atm.; *Reamuria palaestina*, 203 atm.).

Intense salinization of soil, detrimental to very many plants, stimulates growth of the halophytes and improves their vitality. Varied conditions of natural salinization have developed various biochemical types of halophytes: chloride halophytes, chloride-sulphate halophytes, and organo-mineral halophytes (Keller 1940). Halophyte shrubs of genera *Halocnemum*, *Kalidium*, *Halostachys*, *Seidlitzia*, and others are typical representatives of this group (fig. 4). Halophyte shrubs have extensive distribution; their distribution areas often lie within several landscape zones, from the temperate to the tropical.

2. Psammophyte shrubs are plants that grow in moving and overgrown sands. Under the conditions of a mobile substratum they often become covered with sand, but they do not always perish even when thus buried. Should the sand over them become slightly moistened, numerous adventitious roots start developing on the branches. Several factors contribute to intensified growth, so that the branches rapidly take root. The burial of plants under moving sands affects the anatomical structure of the plant stem and roots. The change consists in the approximation of the buried stem structure to that of the root. When plants are covered with sand during growth, the mechanical action of sand crushes their vessels and causes considerable skewing of the plant members.

Psammophytes have a unique root system: their lateral roots usually extend along slopes of barkhan chains for 25-30 m. In depth they extend sometimes to 20-25 m., reaching the capillary backwater and ensuring a sufficient supply of moisture.

During sand shifting, wind blows the soil out from under the roots, which become partly exposed and lie on the surface of the barkhans. The roots do not perish, however; they are protected against the burning sun rays by a thick crust (*Calligonum*, *Ammodendron conollyi*, and so on) or by a coating of cemented sand particles (*Aristida*). Typical representative of psammophytes are the moving sand shrubs of the genera Calligonum, *Caragana*, *Hedysarum*, *Eremosparton*, *Ammodendron*, and others.

3. Petrophyte shrubs, plants that grow in rocky and stony locations on mountains in the arid zone. Their habitats have fairly good moisture conditions because rainwater accumulates in deep fissures into which the shrubs' root systems reach. Therefore most petrophyte shrubs have a xero-mesophytic appearance, e.g., larger leaves. Such plants include species in the genera *Zygophyllum*, *Tetraena*, *Ammopiptanthus*, *Rhamnus*, and others. (fig. 5).

4. Gypsophyte shrubs grow over the sheet structural plains and plateaus. These habitats are the most severe because of the extreme dryness and salinity of soil (sulphates and carbonates). All gypsophyte shrubs are low, small-leaved or leafless, and are characterized by high osmotic pressure and high content of water-soluble salts in the leaves. Typical representatives of gypsophytes are species in the genera *Salsola*, *Anabasis*, *Sympegma*, *Hammada*, and others.

5. Mesophyte shrubs are widespread in the steppe zone. Among them can be included species in the genera *Caragana*, *Cerasus*, *Amygdalus*, and *Spiraea*.

Figure 4.--Halophilous shrub Halostachys caspica. *Central Asia.*

Figure 5.--Petrophilous shrub Tetraena mongolica *in Ordos Desert, Central Asia*

Importance of arid climate for accumulation of useful substances in plants

The importance of arid climate for the processes of accumulation of useful substances by plants is very great. In adaptation to a hot climate, plants accumulate in their leaves, flowers, and fruits certain quantities of substances that decrease transpiration and increase heat resistance by decreasing the osmotic pressure of cell sap and retaining moisture in leaves.

Results of investigations devoted to the discovery of internal factors that affect the rate of transpiration of desert plants and their resistance to heat and drought allow the inference that osmotic pressure of the cell sap is of chief importance in these processes. Osmotic pressure decreases the degree of swelling of cytoplasm, increases both the suction power of a cell and the water-retaining capacity of tissues, and thus improves the general resistance of plants against prolonged summer drought.

Ash substances play the main role in the osmotic concentration of cell sap. Sugars also are important components in the sap of desert plants because they partly determine its concentration. Sugar content increases considerably as spring advances toward summer; sugars prevalent then are monosaccharides.

The adventitious organs of most desert plants also contain a considerable amount of oily drops in the parenchyma tissue, of crystals of calcium oxalate and colloid substances in the cell vacuoles of the subepidermic layer and the exodermis. The content of all these substances increases during the hot period of summer.

All of this enables the accumulation in plants of several substances that are of practical interest to man. The biogenesis and the role in plants of alkaloids, ethereal and fatty oils, tanning, resinous and other substances are varied. Their physiological importance in plant life is many-faceted.

All the substances just mentioned presumably take part in metabolism, probably during special critical periods in the life of plants growing under extreme environmental conditions, such as the high temperature of dry air, deficiency of available soil moisture, extreme dryness of air, and soil salinity. Therefore it is under arid conditions that we encounter numerous plants that contain many chemical substances useful to man. These substances should be regarded as reserves for various purposes, such as increasing plants' resistance against unfavorable environmental conditions. Biochemists have not yet completely studied all these processes. For instance, some biochemists studying the substances used in tanning believe that these are additional nutritives, just as starch and fats are. Others think these substances play some protective role.

Resins in the ligneous woody part of some shrubs aid the accumulation and storage of moisture that is necessary during dry hot periods. Ethereal and fatty oils can be regarded as power resources.

The character of substances derived from plants is often closely connected to their systematic position. Thus, for instance, ethereal oils are characteristic of some species in the Labiatae family; tanning substances come from the Polygonaceae, Salicaceae and Tamaricaceae families. Most representatives of Ephedraceae, Berberidaceae, and Chenopodiaceae families contain alkaloids, while many species of Caryophillaceae contain saponins or glucoside-saponins. The Rosaceae family has characteristically high content of glucosides, organic acids, and sugar in their fruits.

The useful substances contained in the plants of the Leguminosae family are numerous and varied. Their fruits, leaves, and bark contain glucosides, alkaloids

(cytisine, engeteine, pachycarpine, and so forth), and peculiar resinlike carbohydrates: bassorine, arobine, mannan, and so forth, as well as tanning substances and pigments.

The composition and quantities of substances that can be collected from plants depend on the phase of the plant's development and the conditions of its growth--climate, soil, and so forth.

Uses of shrubs

The wild shrubs in arid areas have been used by local populations from time immemorial. People have used individual parts of plants (e.g., fruit, flowers, leaves, branches) and whole plants. Intensity of the utilization of shrubs has varied. For a long time, utilization was limited to local demand, but in time raw materials began to be exported from arid areas. In recent decades, industrial plants have become interested in the vegetal resources of arid areas.

Nearly all shrubs in Asia's arid zone are useful for some purpose or other. It is manifestly impossible to list all these shrubs and their varied uses; so a few illustrations will have to suffice.

By the character of their utilization, these wild shrubs can be divided into the following groups: medicinal, vitamin-bearing, tannous, pigmentous, resinous, salt-bearing, fruit- and berry-bearing, decorative, and usable as fodder and fuel.

Medicinal and Pharmaceutical

The shrubs used in folk medicine nd in the pharmaceutical industry are numerous. They grow in all arid areas from the severe deserts of Middle and Central Asia to the tropical deserts of India. Their principal medicinal substances are alkaloids accumulated in different organs of the plants.

The shrub *Ephedra equisetina* grows extensively in mountain deserts and semideserts in all arid areas of Asia. It contains the alkaloid ephedrin ($C_{10}P_{15}ON$) and its isomers and derivatives. This alkaloid is obtained from green unlignified twigs. Alkaloid ephedrin is present in all *Ephedra* species, but *E. equisetina* has the largest content--up to 3 percent. In Central Asia, *E. shenungiana* contains up to 1.3 percent.

Ephedrin is used as ephedrinum hydrochloricum to relieve cases of drastic decrease in arterial pressure, bronchial asthma, and toxic effects of narcotics and soporifics. Its effect is similar to that of adrenalin (Adrenalinum).

Salsola richteri, a tall psammophyte shrub (fig. 6), grows extensively in semi-shifting and over-grown sands of Middle Asia and Iran. Leaves, flowers, and fruit all contain the alkaloids salsolinum ($C_{11}H_{15}NO_2$), salsolidinum, and salsominum (up to 0.3 percent), which are raw materials for the production of medicines. Salsolidinum hydrochloricum and Salsolinum hydrochloricum are used in medical practice for decreasing arterial pressure and improving the general condition of patients suffering from the first stage of hypertension.

The shrub *Smirnovia turkestana* grows up to 1 m. high and is widely spread in sand deserts of Central Asia. Its flowers and leaves contain the alkaloids spherophysinum, smirnovinum, and smirnovininum. Preparations from these alkaloids greatly decrease hypertension and are used for first and second stage hypertension and for relieving blood vessel spasms.

Nanophyton erinaceum, a low-growing (15-20 cm.) shrub, resembles dense pillowlike stiff sod. Up to 0.1 percent of 2.6 dimethyl-piperidine and 1.2 trimethyl-piperidine alkaloids are collected from the overground part of the shrub. These alkaloids are

Figure 6.--Psammophilous shrub Salsola richteri. *Kara-Kum, Middle Asia.*

the base for the nanophyne preparation, which is used for the first and second stage hypertension.

Berberis heteropoda and *B. sibirica* grow in semidesert mountains of Central and Middle Asia. Their bark and roots contain the alkaloid berberidin used as styptic medicine.

Medicinal shrubs are also common in the subtropical and tropical zones of the arid part of Asia. These include some resinous species of acacias (e.g., *Acacia arabica*). The leaves of *Cassia obovata*, *C. acutifolia*, and *C. angustifolia*, which grow in the Arabian Peninsula, contain the antiriglucosides senna emodin, senna rhein, and others, and have long been used as laxatives (*Folium sennae*). Aqueous (*Infusum foliorum sennae*) or a composite (*Infusum sennae compositum*) infusion is used.

Other alkaloid-bearing shrubs produce materials used for preparing insecticides. Species of *Anabasis*, growing in deserts and semideserts of Middle and Central Asia, can be included among these. For example, the green leaves of *A. aphylla* contain the alkaloids anabasin, aphyllin, and aphyllidin (up to 12 percent), which are used in manufacture of anabasin-sulphate insecticide. The principal alkaloid, anabasin ($C_{10}H_{14}N_2$), has no oxygen and is an isomer of nicotine. Anabasin sulphate is widely used against agricultural pests.

Methyl-anabasin, a derivative, has an invigorating effect on respiration centers and is used in combination with cophein.

Vitamin Producers

Some arid area shrubs, notably wild roses, produce vitamins. The high content of Vitamin C in wild roses is well known. In mountainous regions of Middle Asia, *Rosa lacerans* and *R. beggeriana* have high vitamin content. *R. maximowicziana* and others in Central Asia are vitamin producers.

Before leaving discussion of medicinal shrubs we should note that old manuscripts about Chinese, Tibetan, and Arabian medicines (e.g., *Notes of Medicinal Plants* by Ish-sheng, 16th century) reflect extensive experience of ancient peoples in the use of these plant materials. A study made in the U.S.S.R. of collections of medicinal plants used in Tibetan medicine revealed approximately 500 species. One-fifth of these were from Indian flora, another 20 percent from the Chinese, and about 10 percent were brought from Iran; the other 50 percent grow in Mongolia and eastern Siberia. Many of these plants have been accepted by scientific medicine and have been introduced into pharmacology.

Tanning Substances

Shrub substances used in tanning are also widespread in arid areas. These include, in the sand deserts of northern Middle Asia, *Salix rubra*, *S. caspica* and, in the southern part, the psammophilous *Calligonum* shrubs. In ancient river valleys and deltas of the temperate zone, halophylous *Tamarix* shrubs are common; in mountainous regions, *Ephedra* species are used locally for tanning leather.

Young leaves, twigs, and flowers of *Tamarix*, *Calligonum*, and *Ephedra* are rich in tanning substances. The galls of *Tamarix* have numerous tannides; in *T. hispida*, tannide content may be as much as 14 percent. Adventitious twigs of *Calligonum* may have up to 15 percent tannides, and green twigs of *Ephedra equisetum* may have 14 percent. In desert-like savannas in the subtropical and tropical zones of Asia, several acacia shrubs contain tanning substances. These include *Acacia jaquemonti* and *A. leucophlea* in Rajasthan (India) and *A. arabica*, *A. senegal*, *A. decurrens*, and others in Arabia. The bark of *A. arabica* contains a high percent of tanning substance, and the bark of *A. decurrens* contains up to 40 percent (S. Kachalov 1970).

Tanning substances are easily soluble in both cold and hot water and have a strong astringent flavor. With iron oxide salts in a neutral or slightly acid medium, they produce black or green pigmentation. Therefore the inhabitants of arid areas habitually use them for dyeing cloth.

Resin Producers

Of the several species of resinous shrubs found in semidesert areas of the Iranian upland, the most valuable are the *Tragacantha* of the Leguminosae family, which have wide distribution. They grow on dry debris-covered mountain slopes up to 2,500 to 3,000 m. elevation. The most resinous is *T. piletoclada*, a low thorny shrub that gives a light colored resin (ketira, gum-dragon) produced by making cuts on the trunks of shrubs. This resin consists mainly of slightly soluble bassorine (60-95 percent), which swells greatly in water, and of water-soluble arabine (5-10 percent), which increases in volume several times tenfold.

In the subtropical and tropical zones, the resinous shrubs are *Acacia arabica*, *A. senegal*, *A. stenocarpa*, *A. seyal*, *A. decurrens*, *A. horrida* (in Africa), and *A. leucophlea* (in India).

The principal quantity of tragacantha resin is collected in mountain deserts and semideserts of the Iranian upland. The centers for collection in Iran are Isfahan,

Shiraz, Kermanshah, Kerman, Semnan, and Shahrud. In the 1940's and 1950's Iran exported as much as 4,000-5,000 tons annually.

Resin is a means of accumulation and storage of moisture and protects shrubs against mechanical damage to external tissues. It is used as an emulsifier in medicine and as a binder in the production of pellets, pills, and lozenges. It is also widely used in the textile industry in printing patterns on chintzes; also for manufacturing candy, glue, water colors, and perfumes.

Oils and Pigments

Plants that produce ethereal oils are very characteristic of arid areas, and there are many of them; some have been known since antiquity. Ethereal oils are accumulated mainly in leaves and flowers.

Pigmentous shrubs have been known and used by local populations for a long time. Green twigs of *Ephedra* spp. give yellow coloring to cloth, and leaves and young twigs of *Berberis* spp. dye cloth into golden and red-yellow colors. Green fruit of *Paliurus spina-christi* dye silk and wool into pink, green, buff, and pinkish-lilac colors. Green twigs of *Tamarix* dye cloth yellow and yellow-green. In subtropical and tropical regions of Asia, leaves of *Lawsonia inermis* and other shrubs are used for dyeing.

Salt Producers

Halophilous shrubs have many water-soluble salts in their cell sap and hence are good raw material for making soda and potash. These substances are still produced by primitive methods for home use. Among such shrubs are *Haloxylon* spp., *Kalidium* spp., *Salocnemum strobilaceum*, *Anabasis* spp., *Halostachys* spp., *Salsola arbuscula*, *S. gemmacens*, and others.

Edible fruits of some shrubs are used by many local populations. In the steppe zone the *Cerasus* fruit is widely used for food, while in the Indian savanna and the south of Iran the fruit of *Ziziphus nummularia*, and in the deserts of Central Asia the fruit of *Nitraria* are eaten regularly. Inhabitants of mountain deserts and semideserts of Asia make nougat and tea substitutes from the fruits of *Berberis* spp. and wild rose.

Fodder and Fuel

Moreover, numerous shrubs in the arid areas provide good fodder for all animals. During droughty periods in the savannas of western India, shrubs are almost the basic fodder for sheep and camels. Here the thickets of shrubs appear to be cut to one level from below--to the height of the camel's head. For thousands of years, shrubs have been the principal fuel in arid areas of Asia.

Psammophyte shrubs in the deserts and semideserts of Asia are widely used for reinforcing and forestation of moving sands. The most valuable of these are *Calligonum caput-medusae*, *C. arborescens*, *Salsola richteri*, *S. paletzkiana*, *Haloxylon persicum*, *H. aphyllum*, *Caragana microphylla*, and *C. korshinskii*.

Acquaintance with different deserts of the globe, through both travel and literature review, allows me to say that the uses of desert shrub vegetation have much in common. Although species in widely separated deserts are quite different systematically, local populations use them for the same purposes. What cares an American Indian of the Sonoran desert whether the creosote shrub *Larrea tridentata* belongs to the family Zygophyllaceae; or a nomad of an Asian desert about *Haloxylon aphyllum*

belonging to the Chenopodiaceae family? Both tribesmen use the stems and branches of these shrubs as fuel for their hearths with equal success. A native of India tans skins with an infusion from local species of *Acacia*, while the nomads of Central Asia perform the same operation with extractions from the bark of *Salix* or branches of *Tamarix* and *Ephedra*.

More extensive use of wild shrubs of arid areas has been prevented in recent years by progress of science and technology. Successes of the chemistry of polymers and organic chemistry permit manufacture of analogs of the useful substances of organic origin at very low costs. In recent decades, numerous dyeing, tanning, and medicinal substances have been synthesized. As a result, industrial utilization of wild shrubs as raw materials decreased in several countries, and only local populations keep using them.

Proposals for further work

Further systematic study of the shrubs of arid areas of Asia should continue in the following specific directions to meet recognized needs.

1. Take inventory. List all species and catalog their systematic position and ecological features.

2. Chart geographic distribution. Delineate areas occupied by individual species and map occurrence of shrub vegetation groups.

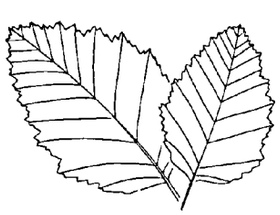
3. Study productivity. List useful substances obtained from whole shrubs and from individual parts (leaves, twigs, roots, and so forth).

4. Evaluate useful substances. Determine their chemical composition and list their known uses.

5. Compile literature. Collect publications, including special monographs, about useful shrubs in all regions and countries.

6. Develop improved methods for cultivating the most valuable shrubs.

Probably this suggested program of study of the shrubs of arid areas of Asia would be acceptable for studying shrubs in other arid areas of the globe.



South America

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South America, with an area of 18 million square kilometers, includes varied floristic and vegetational territories that range from the Amazonian Hyleaea to the Pacific Coast deserts. Among areas so diverse in geographic features, those in which shrubs dominate or at least characterize the landscape are an important fraction of the total. These woody life-forms, either chamaephytes, nano-, or microphanerophytes (Ellenberg and Mueller-Dombois 1967), are peculiar structures from two points of view--resource utilization and distribution and production of biomass that man has cropped and continues to crop in various ways.

The shrub is the result of adaptation of organic forms to the resources and conditions of particular habitats. Man has progressed less in learning how to manage shrubs than he has in managing either herbs or trees. In most areas where shrubs are used for fodder, management has not gone beyond the exploitive phase; its intent has not been to introduce management techniques or manipulations that would increase productivity. This is the situation in most arid and semiarid territories where shrubs are an important source of forage or are the only source available.

Several species of small trees and shrubs grow in the xerophytic forests and deserts of the Caribbean region and in Colombia and Venezuela. Drought prevails for 8 to 9 months of each year in these areas. Rainfall amounts to 300 to 600 mm. per year, and the average temperature is about 20° C. Besides the cují or trupillo (*Prosopis juliflora*), the species of shrubs most commonly found here are *Cercidium praecox*, *Capparis coccolobifolia*, *Castela erecta*, and *Malpighia punicifolia* (Hueck 1966).

The Campos Cerrados, usually called simply Cerrados, is dominated by numerous low evergreen woody plants (Ferri 1963). The Cerrados cover a large area in east-central Brazil. The subhumid tropical climate is broken by a period of 3 to 5 months each year when rainfall is practically nil (Paes de Camargo 1963; Hueck 1966). According to Hueck, distinction between tree and shrub forms in this area is difficult; one species is represented by plants that grow 3 to 5 m. high on heavy soils, but only to 1 m. on sandy soils. The Leguminosae family has the most species here, but the Vochysiaceae is more abundant even with fewer species. Toledo Rizzini (1963) lists 17 species in the shrub stratum in the Cerrados; the more important are *Alibertia sessilis*, *Bauhinia bongardii*, *Brosimum gaudichaudii*, *Camptosema coriaceum*, *Caesaria sylvestris*, *Copaifera oblongifolia*, *Himanthus obovata*, and *Miconia albo-rufescens*.

The vegetation unit called Caatinga in northeastern Brazil differs from the Cerrados in several important respects. Severe droughts sometimes persist for 3 to 6 months, and the average temperature is usually higher than 26° C. Shrubs in the Caatinga have a conspicuous xerophytic character and nearly all of them are leafless during the dry season. Families and genera found most frequently here are: Euphorbiaceae, *Euphorbia* and *Croton;* Annonaceae, *Anona* and *Rollinia;* Polygonaceae, *Coccoloba;* Capparidaceae, *Capparis;* Flaccourtiaceae, *Prockia;* Sterculiaceae, *Helicteres;* and Solanaceae, *Brunfelsia*.

The coastal desert along the Pacific Ocean in Peru and Chile is far from uniform and shows considerable environmental diversity. Alberts (1947), reporting on fodder resources, stated that several vegetation types can be distinguished here. In the northern rainwatered zone, a rainy season comes between January and March but the rainfall regime is very irregular. Chief browse plants include *Acacia macracantha, Capparis scabrida, Caesalpinia corymbosa,* and *Cordia rotundifolia.* Where soil moisture is adequate, nearly all these species grow to be large trees if they are protected from grazing.

Further south in Chile in this same coastal desert country, between Iquique and Copiapo, the dominant shrubs are *Lycium chanar, Bahia ambrosioides, Proustia tipia, Ophryosporus foliosus,* and *Euphorbia lactiflua* (Jorquera 1963). Another vegetation type, called "jaral costero," includes the shrubs: *Balbisia peduncularis, Euphorbia lactiflua, Skytanthus acutus, Oxalis gigantea, Ephedra andina, Heliotropium stenophyllum* and *H. floribundum,* and *Polychirus littoralis.* In several other vegetation types in this region, all of them strongly xerophytic, shrubs are conspicuous. This is true in the *tamarugal,* the desertic *jaral,* the Andean steppe, and the *llaretal.* Besides *Prosopis tamarugo,* the plant for which the extensive plateau (nearly 500 km. from north to south) was named, other common species are *Ephedra andina, Lippia trifida* and *L. deserticola, Proustia baccharioides, Senecio* spp., *Cassia acutifolia,* and several species each of *Baccharis, Fabiana, Adesmia, Laretia,* and *Azorella.*

In southern Chile, in more mesophytic communities, several species of thorny shrubs appear; among these are *Trevoa trinervis, Colletia spinosa, Proustia pungens,* several species of *Adesmia,* and *Fabiana imbricata, Gutierrezia paniculata.*

The Chaco region, an extended territory covered mostly by a strongly xerophytic forest, includes diverse floristic-structural units and characteristic species as follows: *algarrobo*-forest, *Prosopis alba* and *P. nigra; quebracho*-forest, *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco;* palm savanna, *Trithrinax campestris* and *Copernica australis;* jume-scrub, *Suaeda divaricata* and *Allenrolfea vaginata;* and the *palosanto*-forest, with *Bulnesia sarmientoi.* Several shrubs form part of the plant communities in these vegetation units. Some information has been published about their use as fodder and their role in species succession.

In one of the few publications on this subject in Latin-American literature, Morello and Saravia Toledo (1959) recorded significant information about the diet of cattle in the western part of the Chaco Forest in Argentina. Cattle feed on grasses and low shrubs during summer and fall, notably species of *Beloperone, Justicia,* and *Ruellia* (the so-called "uchu-yuyos") in the Acanthaceae family. During the dry winter season, livestock browse on trees and shrubs, particularly *Atamisquea emarginata, Maytenus spinosa, M. vitis-idaea, Grabowskia duplicata, Achatocarpus nigricans, A. Praecos, Castela coccinea, Capparis retusa,* and *C. tweediana.* According to these authors cattle eat fruits of several small trees and shrubs (e.g., *Geoffraea decorticans* and *Prosopis torquata*) during the season following the month of July. Ragonese (1967) reported that cattle in this region eat the fruits of *Acacia aroma, Prosopis vinalillo,* and *P. algarrobilla.*

Heavy grazing by cattle and goats in Chaco has resulted in serious disturbance of structural, floristic, and ecological aspects. The most palatable shrubs disappear, become cushionlike, develop large xylopodia, or repeatedly produce regrowth from old roots--all typical responses to heavy grazing. Consequently, some unpalatable species come in and replace the departed desirable species after the environment has been altered by overuse. In this group, Morello and Toledo include *Vallesia glabra* and *Cassia aphylla;* however, Covas claims that the latter species is browsed regularly in the province of La Pampa, Argentina.

The vegetation unit named Monte in Argentina is a desert scrub that extends over a wide area. Rainfall usually does not exceed 200 mm. per year, and summer is the rainy

season. Temperature extremes range between 45° and -15° C., and the annual average temperature ranges between 13° and 19° C. Because of its ecological diversity, this area necessarily includes many and varied plant communities. As dominants, species of the genus *Larrea* are seen most frequently. *Larrea divaricata*, *L. cuneifolia*, and *L. nitida* are three evergreen shrubs that keep at least some leaves during even the most severe droughts. Livestock generally do not browse these shrubs when conditions are normal, but some evidence indicates that *Larrea cuneifolia* has been intensively browsed to the point of becoming dwarfed. Other evergreen shrubs seen frequently in Monte are *Zuccagnia punctata* and *Atamisquea emarginata*. The most important deciduous species probably are *Bulnesia retama*, *Plectrocarpa rougesii*, *Bougainvillea spinosa*, *Prosopis alpataco*, *Prosopidastrum globosum*, *Ximenia americana*, and *Lycium chilense*. Aphyllous or nearly aphyllous shrubs and their photosynthesizing stems are represented by *Monttea aphylla*, *Ephedra ochreata*, *Neosparton aphyllum*, and *Cassia aphylla*.

As for many other arid or semiarid territories in South America, there is virtually no published information about the use and value of shrubs in the Monte. Although shrubs produce most or all of the available biomass, little has been written about degree of livestock preference, fodder value, or growth response to browsing (Ragonese 1967; Morello 1958). However, in 1938 Monticelli reported the use of some shrubs in the southern part of the Monte. He stated, among other things, that livestock eat *Ephedra ochreata* eagerly and that it does not contain ephedrin; he also reported that some people claim this plant imparts an undesirable flavor to meat. Báez (1938) in writing about *Verbena erinoides*, a shrub common in the central part of Monte, stated that it provokes costiveness. Soriano (1949) mentioned *Baccharis darwinii*, a low shrub living in the southern part of Monte, and reported that its young twigs are very soft and so are heavily clipped by sheep. Overgrazed plants never attain normal size and it is often difficult to identify them.

Puna province is a phytogeographic territory that occupies a high plateau (3,500 to 4,500 m.o.s.) that extends from southern Peru to northwestern Argentina and embraces part of western Bolivia and northern Chile (Cabrera 1953). From its physiography, this territory can be classed as semidesert. Rainfall changes from north to south and from east to west between depths of 50 and 500 mm. per year; average temperature reaches 10° C. The dominant life-form is low shrubs, from 0.5 to 1 m. high. Dominant shrubs in the climax vegetation of this region are *Fabiana densa*, *Adesmia horridiuscula*, *Tetraglochin cristatum*, *Psila boliviensis*, *Acantholippia hastulata*, and *Verbena seriphioides* (Cabrera 1953).

Ragonese (1967) reported studies by V. Cabezas that showed livestock preference for *Adesmia horridiuscula*, *A. spinosissima*, *Parastrephia lepidophylla*, *Tetraglochin cristata*, and *Cassia hookeriana*. Average carrying capacity of dry sites in the high plateau at Jujuy, Argentina, is about one sheep to three-fourths ha.

The Patagonian semidesert extends through southern Argentina from the eastern Andean piedmont to the Atlantic coast. In this territory rainfall does not exceed 300 mm. per year, and the average temperature lies below 13° C. In this wide area we find plant communities that contain no shrubs, others in which they are commonly intermingled with tussock grasses, and in still others where shrubs dominate. Where shrubs predominate, they give the landscape its character. They can compose a very flat stratum near the soil surface if the dominant species is *Nassauvia glomerulosa*, or a desert scrub stratum 1 m. or more high if *Verbena tridens*, *Nassauvia axillaris*, *Anarthrophyllum rigidum* or *Pseudoabutilon bicolor* predominate.

The most common shrubs here usually keep their leaves the year around. Their species include *Mulinum spinosum*, *Senecio filaginoides*, *Chuquiraga avellanedae*, *Colliguaya integerrima*, *Berberis cuneata*, *B. heterophylla*, and other species just mentioned.

In *Mulinum spinosum*, the color and the amount of leaves in the hemispheric bushes can serve as a gross indicator of soil moisture. Color can vary from a deep green to a

brownish yellow, and amount can vary from a sheet of leaves that covers the whole cushion to a few leaves that remain at ends of branches. Some shrub species (e.g., *Lycium chilense* and *Adesmia campestris*) are deciduous, but others (*Ephedra ochreata, E. frustillata, Trevoa patagonica,* and *Stillingia patagonica*) are aphyllous.

Distribution of these shrubs through the vast Patagonian territory follows the patterns of different communities characteristic of the five districts into which the phytogeographical province has been divided (Soriano 1956a). Vegetation in all these communities is used as forage for sheep. Livestock numbers current on ranches in the different districts range from 500 to 2,500 sheep per square league (2,500 ha.) (Soriano 1956b). Most of the shrubs already mentioned contribute to the diet of sheep in Patagonia, as evidenced both by direct observations of animals browsing or by noting the heavily clipped and deformed plants. These types of evidence allow us to infer relative preferences. Notwithstanding, some plants protected by exclosures must be observed to determine that the common habit shown by a species is not the normal habit corresponding to prevailing climatic and edaphic conditions. This can be true for *Tetraglochin caespitosum* and even for *Verbena ligustrina* when grazing pressure is not too high.

Commonly, sheep clip the leaves or, more frequently, the young leafy twigs of certain shrubs such as *Adesmia campestris, Lycium chilense,* and *Nassauvia glomerulosa.* It is generally believed that sheep eat the umbels of *Mulinum spinosum*; they also consume aphyllous shrubs such as *Ephedra ochreata* and *Prosopidastrum globosum.* Sheep utilize not only the leaves and twigs of such palatable species as *Atriplex sagittifolium* but also the branches and woody stems. Often the plant cover in the halophytic communities in which this species grows is very low; so overgrazing is common. Conversely, some other shrubs are never touched by livestock; e.g., *Senecio filaginoides, Chuquiraga avellanedae, Sapium patagonium,* and *Colliguaya integerrima*; some evidence suggests that these last two species are poisonous.

Some of the Patagonian shrubs mentioned above provide excellent forage, and obviously they deserve much more attention from both agronomists and plant breeders. Propagation of *Verbena ligustrina, Lycium chilense, Ephedra ochreata, Pseudoabutilon bicolor, Atriplex sagittifolium,* and *Trevoa patagonica* could be a worthwhile objective in Patagonian range improvement programs. This is valid not only for these species of this particular region but also for those in other semiarid territories of South America where shrubs provide fodder.

It is possible to foresee technological advances that could improve productivity in territories where drought now seriously limits it. However, such expectations cannot justify failure to develop or to speed up action to make better use of resources made available by Nature through long organic revolution. To see the maquis or the desert scrub as a plant system that is neither grassland nor forest merely abandoned to overgrazing because it cannot economically be changed into either grassland or forest is to accept a sort of naive fatalism. Against such thought and action the resources of science and technology should be mobilized, together with sound measures developed within the social and economic spheres of the regions concerned.

North America

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Outside of the arid and semiarid regions, shrubs are in many respects the second-class citizens of the North American plant world. Throughout the major forest and grassland areas shrubs are usually given minor attention by botanists who tend to emphasize the dominants. In the northern coniferous forest, they are the plants that occupy the acid habitats and occur in natural or manmade openings. Few can tolerate the conditions in climax forests. In the deciduous forest, shrubs sometimes receive considerable attention by horticulturists and nature admirers because of their attractiveness. In the Southeast, they exist largely between the tree-dominated forests and the forb-dominated wet lands. In the grasslands, they are largely restricted to marginal habitats and areas disturbed by man. It is only in the relatively dry areas of North America, especially in the West and Southwest, that they become the plants that characterize the plant communities.

Shrubs also have a problem in establishing their identity. They belong to the category "woody plants," but at times they may be indistinguishable from trees. Many descriptions read "shrub or small tree." However, the characteristic of size does not clearly set them apart because some shrubs may be larger than some trees, especially young trees and trees limited in size by arctic-alpine conditions. Neither does the multiple stem categorization always apply because some plants commonly considered as shrubs may have a single main trunk.

The distribution of shrubs in North America can be divided into regions based on broad phytogeographic relationships. These include: (1) Arctic-Alpine; (2) Northern Coniferous Forest; (3) Eastern Deciduous Forest; (4) Southern Coastal Plain; (5) Central Grassland; (6) Rocky Mountain; (7) Great Basin; (8) Broad Sclerophyll Region of western North America; (9) Deserts of United States and Mexico; and (10) Mesic Regions of Mexico including mountains and lowlands.

Although this is a somewhat arbitrary arrangement, it follows in general the classification of Harshberger (1911), Shreve (1917), Livingston and Shreve (1921), Shantz and Zon (1924), Weaver and Clements (1938), Leopold (1950), and Küchler (1964). The plant nomenclature used is largely that used in specific publications cited.

Regions where shrubs are subordinate to other life forms

The arctic-alpine

Shrubs reach their most northerly distribution in the arctic tundra, occupying the broad zone between the tree limit and the region of perpetual snow. According to Weaver and Clements (1938), they are largely restricted to protected slopes and valleys, occurring as a postclimax of heaths, willows, and birches. Important genera include crowberry (*Empetrum*), bog rosemary (*Andromeda*), Labrador tea (*Ledum*), *Rubus*, alder (*Alnus*), birch (*Betula*), willow (*Salix*), *Arctostaphylos*, *Cassiope*, *Vaccinium*, and *Rhododendron*. The arctic shrub communities border the northern coniferous forest and many of the genera are found within the forest, especially in openings and successional stages leading from bog to a forest climax.

Northern coniferous forest

In the coniferous forest, the greatest concentration of shrubs is found in natural or manmade openings, bogs, and primary or secondary successional states. A few shade-tolerant species occur as a scattered forest understory.

Among the important shrub species of the northern coniferous forest listed by Oosting (1956) are Hobblebush (*Viburnum alnifolium*), witherod viburnum (*Viburnum cassinoides*), speckled alder (*Alnus incana*), bog rosemary (*Andromeda glaucophylla*), cassandra (*Chamaedaphne calyculata*), rhodora (*Rhododendron canadense*), black crowberry (*Empetrumnigrum*), cloudberry (*Rubus chamaemorus*), lowbush blueberry (*Vaccinium pennsylvaniana*), and cowberry (*Vaccinium vitis-idaea oxycoccus*).

The heath stage of the bog succession is made up of shrubs able to endure poor aeration and acidity--species of laurel (*Kalmia*), Labrador tea (*Ledum*), cassandra (*Chamaedaphne*), crowberry (*Empetrum*), bog rosemary (*Andromeda*), *Rhododendron*, and *Vaccinium*.

The margins of the openings are occupied by taller species--speckled alder (*Alnus incana*), green alder (*Alnus crispa*), witherod (*Viburnum cassinoides*), squashberry (*Viburnum pauciflorum*), beaked hazelnut (*Corylus rostrata*), red osier dogwood (*Cornus stolonifera*), red chokeberry (*Pyrus arbutifolia*), swamp birch (*Betula pumila*), and willow-leaf spiraea (*Spiraea salicifolia*).

The most common shade plants are dwarf or creeping shrubs, but species of *Alnus*, *Corylus*, and *Spiraea* also occur.

Bogs that may occur either in the northern coniferous forest or in the eastern deciduous forest are noted for their shrub populations in later successional stages. Gates (1942) describes a bog succession in lower Michigan in detail starting with cassandra (*Chamaedaphne calyculata*), downy bog-rosemary (*Andromeda glaucophylla*), pale laurel (*Kalmia polifolia*), Labrador tea (*Ledum groenlandicum*), and small cranberry (*Vaccinium oxycoccus*), through the bog-shrub association including chokeberries (*Aronia* spp.), mountain-holly (*Nemopanthus mucronata*), bog willow (*Salix pedicellaris*), swamp birch (*Betula glandulifera*), and speckled alder (*Alnus incana*) followed by larch (*Larix*) association or spruce forest.

Eastern deciduous forest

Most publications covering the ecology of the eastern deciduous forest place major emphasis on trees; discussion of shrubs often is tucked away in scattered paragraphs or in a sentence or two intermixed with details of the forest canopy. However, shrubs do have an important place in the deciduous forest even though they are over-

shadowed by the dominant trees. Braun (1950), in her monograph on the deciduous forests, does not give shrubs much attention. In a paper covering the forests of the Cumberland Mountains (1942) she does, however, discuss in detail shrubs and woody climbers as related to terrain and the forest canopy.

Whittaker (1960), fully recognizing the importance of shrubs in the flora of the Great Smoky Mountains, listed 35 important species including four rhododendrons (*Rhododendron maximum, R. calendulaceum, R. catawbiense,* and *R. carolinianum*); three species of viburnum (*Viburnum acerifolium, V. alnifolium,* and *V. cassinoides*); and six species of vaccinium (*Vaccinium constablaei, V. vacillans, V. hirsutum, V. stamineum, V. candicans,* and *V. erythrocarpum*).

The forest border on the eastern edge of the central grassland has a rich shrub flora, although most of the shrubs are restricted to rough terrain types. For example, Stephens (1969) lists the following shrubs as occurring along the forest border in Kansas: hazelnut (*Corylus americana*), wild gooseberry (*Ribes missouriensis*), golden current (*Ribes odoratum*), wahoo (*Euonymus atropurpureus*), deciduous holly (*Ilex decidua*), buckthorn (*Rhamnus lanceolata* var. *glabrata*), New Jersey tea (*Ceanothus ovatus*), wolfberry--also called snowberry (*Symphoricarpos occidentalis*), willow baccharis (*Baccharis salicina*), soap weed (*Yucca glauca*), spicebush (*Lindera benzoin*), rough-leaved dogwood (*Cornus drummondii*), swamp dogwood (*Cornus amomum*), lowbush blueberry (*Vaccinium vacillans* var. *crinitum*), buttonball bush (*Cephalanthus occidentalis*), buckbrush (*Symphoricarpos orbiculatus*), prairie rose (*Rosa suffulata*), smooth sumac (*Rhus glabra*), elderberry (*Sambucus canadensis*), leadplant (*Amorpha canescens*), indigo (*Amorpha fruticosa*), prickly ash (*Zanthoxylum americanum*), winged sumac (*Rhus copallina* var. *latifolia*), black raspberry (*Rubus occidentalis*), dewberry (*Rubus flagellaris*), highbrush blackberry (*Rubus ostryifolius*), fuzzy prairie rose (*Rosa setigera* var. *tomentosa*), aromatic sumac (*Rhus aromatica*), poison ivy (*Rhus radicans* var. *vulgaris*), and bladdernut (*Staphylea trifoliata*).

Stephens (1969) described 114 species of trees and shrubs of which 80 percent grow in eastern States, 70 percent in States north of Kansas, 98 percent in the South and Southeast, and 20 percent in the southwestern States.

Southern coastal plain

Although the range of many of the common species in eastern North America extends into the southern coastal plain, the area is not rich in shrubs, which find unfavorable environments in the everglades and similar wet habitats on the one hand and the southern coniferous and hardwood forests on the other. Penfound (1952) described the salt swamps dominated by the red mangrove (*Rhizophora mangle*), and the development of shrub communities on low ridges of brackish streams. Penfound and Hathaway (1938) noted that shrubs were common only in transition between brackish marshes and forests.

Central grassland

The range of many of the shrubs listed by Stephens (1969) for the forest border extends into the central grassland occupying the stream borders and slopes that break the general flat landscape of the prairies and plains. Shrubs also gain a foothold in grasslands where the grass cover is reduced by heavy grazing or other perturbations, especially in the semiarid areas, where many western and southwestern shrubs have extended their ranges.

Tolstead (1947) lists 18 important shrubs in northwestern Nebraska including western snowberry (*Symphoricarpos occidentalis*) making up 37 percent of the total shrub population, skunkbush sumac (*Rhus trilobata*) 21 percent, Arkansas rose (*Rosa arkansana*) 9 percent, poison sumac (*Rhus toxicodendron*) 6 percent, small soapweed (*Yucca glauca*) 6 percent, and fringed sagebrush (*Artemisia frigida*) 5 percent.

Hayward (1928) noted that shrubs occupy an important place in the open woodlands of the Black Hills of South Dakota and are dominant in the chaparral of the foothills. He recognized a sagebrush climax dominated by big sagebrush (*Artemisia tridentata*) and a petran chaparral climax dominated by mountain mahogany (*Cercocarpus parvifolius*) and skunkbush sumac (*Rhus trilobata*).

Aldous and Shantz (1924) listed two shrub communities in the high plains near the western edge of the Central grasslands: *Gutierrezia-Artemisia* and the sandhills mixed association. The former includes broom snakeweed (*Gutierrezia sarothrae*) and fringed sagebrush (*Artemisia frigida*), and the latter includes sand sagebrush (*Artemisia filifolia*), Canada sagebrush (*Artemisia canadensis*), cudweed sagebrush (*Artemisia gnaphalodes*), small soapweed (*Yucca glauca*), and leadplant amorpha (*Amorpha canescens*).

Rocky Mountain region

The vegetation of the Rocky Mountain area is well covered in the literature; many publications emphasize the importance of shrubs. Daubenmire (1943) made particular mention of the small tree and shrub fringe at lower elevations and estimated that the juniper-piñon type covers 76 million acres in the United States. In the Southwest, the oak-mountainmahogany zone may alternate with the juniper-piñon belt or occur below it. In the north, big sagebrush (*Artemisia tridentata*) is the dominant shrub; in the south, a variety of shrubs are found including algerita (*Berberis fremonti*), shrub live oak (*Quercus turbinella*), fourwing saltbush (*Atriplex canescens*), and skunkbush sumac (*Rhus trilobata*). The juniper-piñon type often merges or alternates with a shrubby community termed by some authors as chaparral, a plant community having life forms similar to those of the California chaparral, but lacking some of the dominant California species. Lowe (1964) recognized an oak-pine woodland including larger species and chaparral consisting of a variety of shrubs similar in stature and form to those of California. Both are predominantly made up of broad sclerophyll species including oaks (*Quercus* spp.), several species of *Ceanothus*, *Cercocarpus*, *Rhus*, *Rhamnus*, and *Garrya*, along with Apache plume (*Fallugia* spp.), cliff rose (*Cowania mexicana*), and locust (*Robinia neomexicana*).

Although big sagebrush is usually associated with the Great Basin region, it is also an important species in the Rocky Mountains (Robertson and others 1966; Kelly 1970; Treshow and others 1970).

Shrubs of the Rocky Mountain region have been covered in detail by Kelly (1970) and Treshow and others (1970). Among the important species listed are: Oregon grape (*Mahonia repens*), the honeysuckles (*Lonicers* spp.), mountain love (*Pachistima myrsinites*), rabbitbrush (*Chrysothamnus nauseosus*), dogwood (*Cornus stolonifera*), silver buffaloberry (*Shepherdia argentea*), silverberry (*Elaeagnus angustifolia*), bear berry (*Arctostaphylos uva-ursi*), Gambel oak (*Quercus gambeli*), snowbrush (*Ceanothus velutinus*), serviceberry (*Amelanchier* spp.), hawthorn (*Crataegus* spp.), oceanspray (*Holodiscus microphyllus*), ninebark (*Physocarpus malvaceus*), bush cinquefoil (*Potentilla fruticosa*), chokecherry (*Prunus melanocarpa*), bitterbrush (*Purshia tridentata*), wild rose (*Rosa* spp.), thimbleberry (*Rubus parviflorus*), mountain ash (*Sorbus* spp.), willows (*Salix* spp.), cliff fendlerbush (*Fendlera rupicola*), currants and gooseberries (*Ribes* spp.).

Regions where shrubs are dominant life forms

The last four regions have shrubs at least in part as the dominant species. The Great Basin, or Northern Desert Shrub as designated by Shantz and Zon (1924) has a shrub climax as the name implies. The Broad Sclerophyll Region includes a chaparral climax, and the deserts are noted for the variety of shrubs that give character to the landscape. The mesic regions of Mexico, while more truly low-tree or tall-tree communities, also have very strong shrub elements.

Great Basin

Owing to its extent and the preponderance of shrubs, the Northern Desert Shrub is among the most important shrub areas in North America. Although the ecology of the Great Basin has been the object of many studies, the major emphasis appears to have been on edaphic conditions and the relationship between shrubs of saline and nonsaline soils.

Shantz and Zon (1924) recognized the following three main associations in the sagebrush or Northern Desert shrubs:

Sagebrush *(Artemisia tridentata):*
- Small sage *(Artemisia nova)*
- Scabland sage *(Artemisia rigida)*
- Little rabbitbrush *(Chrysothamnus stenophyllus)*
- Bitterbrush *(Purshia tridentata)*
- Big rabbitbrush *(Chrysothamnus nauseosus)*
- Coleogyne *(Coleogyne ramosissima)*
- Chamiso *(Atriplex canescens)*
- Match weed *(Gutierrezia sarothrae)*

Shadscale *(Atriplex confertifolia):*
- Winter fat *(Eurotia lanata)*
- Hopsage *(Grayia spinosa)*
- Bud sage *(Artemisia spinescens)*

Salt sage *(Atriplex corrugata* and *A. nuttallii):*
- White sage *(Kochia americana vestita)*

Billings (1945, 1949, 1951) conducted extensive studies in the northern desert area and concluded that two major communities should be recognized: one dominated by big sagebrush (*Artemisia tridentata*), often occurring in almost pure stands; the other a shadscale community in which the principal dominants are shadscale (*Atriplex confertifolia*), bud sage (*Artemisia spinescens*), Bailey greasewood (*Sarcobatus baileyi*), and Nevada ephedra (*Ephedra nevadensis*), together with various grasses and forbs. Although the shadscale or salt desert type is typical of the Great Basin, it also extends into South Dakota (Flesland and Whitman (1964).

According to Shreve (1942), *Artemisia tridentata* and *Atriplex confertifolia* share dominance for the Great Basin vegetation. In addition, there are 19 other species for *Artemisia* and 14 for *Atriplex.*

Other prominent shrubs include black sagebrush (*Artemisia nova*), downy rabbitbrush (*Chrysothamnus puberulus*), spiny hopsage (*Grayia spinosa*), blackbrush (*Coleogyna ramosissima*), winterfat (*Eurotia lanata*), greasewood (*Sarcobatus vermiculatus*), Gardner saltbush (*Atriplex nuttalli*), salt sage (*Atriplex corrugata*), bud sage (*Artemisia spinescens*), gray summer cypress (*Kochia vestita*), cottonthorn horsebrush (*Tetradymia spinosa*), bitterbrush (*Purshia tridentata*), Nevada ephedra (*Ephedra nevadensis*), and Torrey ephedra *(Ephedra torreyana).*

Lowe (1964) includes the shrubs listed above, and adds the following for northern Arizona: fourwing saltbush (*Atriplex canescens*), sand sagebrush *(Artemisia filifolia),* broom snakeweed (*Gutierrezia sarothrae*), pale wolfberry (*Lycium pallidum*), New Mexico forestiera (*Forestiera neomexicana*), and Utah serviceberry *(Amelanchier utahensis).*

Warmer regions

The number of species of shrubs found in the southwestern United States (including California and Mexico) is so great that the best that can be done is to mention a few characteristic species and to point out where additional information may be found. Cooper (1922) listed 91 species of importance in the chaparral of California. Benson and Darrow (1954) list over 100 genera in which shrubs may be the only life form or

are an important component. Shreve (1951) discussed 63 important shrub species in the Arizona portion of the Sonoran Desert, 100 species in the mainland Mexico area, and an additional 40 species in Baja California. Gentry (1942) listed 209 shrub species in the vicinity of Rio Mayo, Sonora, between sea level and 9,000 ft.

Shrubs vary from small-tree size down to prostrate or low-growing and sometimes suffrutescent shrubs. Many have spines and nearly all show characteristics that fit in with an arid climate. In addition to broad and narrow sclerophylls, these include small leaves, deciduous leaves, no leaves, and various leaf coverings. The shrubs vary from good browse plants to worthless or even poisonous plants. Some have economic values for wax, rubber, and fiber.

Broad sclerophyll region

The broad sclerophyll leaf is correlated with a climate characterized by winter precipitation and a long dry summer. Some broad sclerophyll species are trees but most are shrubs. In California and elsewhere, there are extensive sclerophyll forests but shrub communities are more important both geographically and economically.

The term chaparral, which is applied to the broad sclerophyll shrub communities of the States of California and Baja California, is derived from the Spanish term "chaparra" meaning scrub oak. Sometimes the term chaparral is applied to related types elsewhere; for example, the broad sclerophyll shrub communities in Arizona, which have many of the same species, but lack important California chaparral species (especially chamise (*Adenostoma fasciculatum*)), and occur in a region having both winter and summer precipitation.

Cooper (1922, lists the most common species in descending order of abundance as follows: chamise (*Adenostoma fasciculatum*), manzanitas [nine species] (*Arctostaphylos*), Photinia (*Heteromeles arbutifolia*), buckbrush ceanothus (*Ceanothus cuneatus*), California scrub oak (*Quercus dumosa*), leather oak (*Quercus durata*), birchleaf mountainmahogany (*Cercocarpus betulifolius*), interior live oak (*Quercus wislizeni frutescens*), California buckthorn (*Rhamnus californica*), and canyon live oak (*Quercus chrysolepis*).

Four species of *Quercus*, 10 species of *Ceanothus*, and nine species of *Arctostaphylos* are listed. *Adenostoma fasciculatum* is by far the most abundant species, often occurring in practically pure stands, while the species of *Arctostaphylos* give a characteristic stamp to the chaparral in many areas.

The California chaparral is subject to recurrent fires that are a menace to rural and urban developments. Because many species have sprouting capabilities, chaparral is able to perpetuate itself at the expense of grasses and other species less resistant to fire (Sampson 1944).

Weaver and Clements (1938) considered chaparral in a broader sense to include not only the "coastal" chaparral that they extended into Nevada and Arizona but also a petran chaparral in Colorado, New Mexico, and Utah with "outliers" in South Dakota and Texas. The major dominants of widest extent are: Gambel oak (*Quercus gambeli*), wavyleaf oak (*Quercus undulata*), mountainmahogany (*Cercocarpus parvifolius*), skunkbush sumac (*Rhus trilobata*), common chokecherry (*Prunus demissa*) and serviceberry (*Amelanchier alnifolia*). In the Southwest, New Mexico locust (*Robinia neomexicana*), cliff fendlerbush (*Fendlera rupicola*), curlleaf mahogany (*Cercocarpus ledifolius*), squawapple (*Peraphyllum ramosissima*), and Gordon mockorange (*Philadelphus gordonianus*), are of importance. In the mountains of central Arizona, pointleaf manzanita (*Arctostaphylos pungens*), and buckbrush (*Ceanothus cuneatus*) mark the transition to the coastal chaparral. In contrast, Plummer (1911) considered the California chaparral to be true chaparral and the community in Arizona a "mock" chaparral.

Deserts of the United States and Mexico

Under the lowest rainfall conditions, desert vegetation tends to present a monotonous appearance. In western Arizona, the vegetation outside drainages may be 90 percent creosote bush and the remaining 10 percent largely the low shrub white bursage (*Fransiera dumosa*). On the other hand, where precipitation is greater and the topography varied, the vegetation structure becomes a complex mixture of trees, shrubs, succulents, and semisucculents.

It is difficult to pick out the most important shrubs because there are many such, but perhaps a few of particular significance may be mentioned. First there is the creosote bush whose scientific epithet may be given as *Larrea tridentata* if the author believes it is distinct from a South American form, or it may be called *Larrea divaricata* having a range including both North and South America. It is the most widespread and abundant desert species. In the driest areas of the Sonoran Desert, it may occur with white or triangle bursage (*Franseria dumosa* and *F. deltoidea*); in the Chihuahuan Desert, it is usually associated with tarbush (*Flourensia cernua*). In both deserts, it gives way to other shrub and tree species under more favorable environmental conditions.

Mesquite (*Prosopis*) is one of the most adaptive woody plants in the desert regions. In bottomlands where the water table is within 50 feet of the surface, it may form an extensive forest of large phreatophytic trees. In Arizona uplands, it may occur as scattered small trees or shrubs having roots extending laterally as much as 100 feet or more near the surface of the soil, competing with grasses and forbs to their detriment. Further east, *Prosopis juliflora* var. *glandulosa* occurs as a shrub with the main woody parts below ground.

The Leguminosae are well represented in the warm desert areas with such genera as *Prosopis, Acacia, Mimosa, Lysiloma, Dalea, Caesalpinia, Parkinsonia, Cercidium, Cassia, Olneya, Erythrina, Calliandra,* and *Krameria.*

The Compositae family is also well represented with such genera as *Brickellia, Gutierrezia, Aplopappus* (or *Haplopappus), Chrysothamnus, Baccharis, Pluchea, Senecio, Tetradymia, Encelia, Flourensia, Viguiera, Zinnia, Hymenoclea,* and *Franseria.*

Shreve (1951) includes six shrubs in his discussion of the commonest plants of the Sonoran Desert: Mescat acacia (*Acacia constricta*), catclaw acacia (*Acacia greggii*), white brittle bush (*Encelia farinosa*), triangle leaf bursage (*Franseria deltoidea*), white bursage (*Franseria dumosa*), and creosote bush (*Larrea tridentata*). In addition to these common species, he mapped the distribution of atamisque (*Atamisquea emarginata*), Bigelow crossosoma (*Crossosoma bigelovii*), smokethorn (*Dalea spinosa*), several species of *Franseria*, and jojoba (*Simmondsia chinensis*). He noted that the number of species of evergreen shrubs was not large, but included creosote bush (*Larrea tridentata*), jojoba (*Simmondsia chinensis*), squawbush (*Condalia spathulata*), desert hackberry (*Celtis pallida*), Sonora cordia (*Cordia sonorae*), jumping bean (*Sapium biloculare*), and *Viscainoa geniculata.*

Other abundant or conspicuous shrubs include condalia (*Condalia* spp.), desert thorns (*Lycium* spp.), saltbushes (*Atriplex* spp.), ephedras (*Ephedra* spp.), sangre de drago (*Jatropha flabelliformus*), and the crucifixion thorns (*Canotia halocantha* and *Koeberlinia spinosa*).

The Chihuahuan Desert, which lies partly in the United States and partly in Mexico, has fewer shrub species than the Sonoran Desert.

Shreve (1942, 1951) lists creosote bush (*Larrea tridentata*), acacia (*Acacia vernicosa* and *Acacia cymbispina*), mesquite (*Prosopis juliflora* var. *correzana*), sand-

paper bush (*Mortonia scabrella*), and tarbush (*Flourensia cernua*) as typical shrubs of the Chihuahuan Desert. He states that in the number of life forms prominently represented in its vegetation, the Chihuahuan Desert occupies an intermediate position between the poverty of the Great Basin and the richness of the Sonoran Desert. Shrubs and semishrubs are the predominant plants, trees are small--confined to streamways or rocky slopes.

Mesic regions of Mexico including mountains and lowlands

Mexico is rich in shrubs that are found in many of the plant communities. Leopold (1950 listed five temperate and seven tropical zones in Mexico where shrubs occur; these are:

Temperate	*Tropical*
Boreal Forest	Cloud Forest
Pine Oak Forest	Rain Forest
Chaparral	Tropical Evergreen Forest
Mesquite Grassland	Savannah
Desert	Tropical Deciduous Forest
	Thorn Forest
	Arid Tropical Scrub

All of these include shrub species; the greatest number are in Chaparral, Desert, Mesquite Grassland, Pine Oak Forest, Thorn Forest, and Arid Tropical Scrub.

Shrubs in the Boreal Forest are either those common to successional stages or those that occur as a scattered understory of shade-tolerant species.

Leopold (1950) reported that the Pine Oak Forest Zone is the most important and largest vegetational type in Mexico. It ranges from an oak scrub bordering the northern desert to pine forests at its upper limits. Standley (1920-1926) lists 112 species of oaks occurring in this zone, of which many are shrubs.

The pine-oak woodlands occur between the oak scrub and the high pine forest. They support many shrub species, including but not limited to species of *Quercus* (Shreve 1942).

Typical California chaparral extends approximately 200 miles down the western coast of Baja California, finally giving way to desert vegetation south of the 30th parallel (Shreve 1936, 1951). A large number of California chaparral species extend into Baja California and reach the limit of their distribution in this area. There is also a plant community closely related to the California chaparral along the western base of the Sierra Madre Oriental in Nuevo Leon (Muller 1939). This bush type includes species of *Rhus*, *Ceanothus*, *Cercocarpus*, *Arbutus*, and *Arctostaphylos*.

The Tropical Cloud Forests, Rain Forests, and Evergreen Forests all include shrubs as an understory and in openings, but they are of minor importance.

The Savannah type occurs on coastal plains or in marshy interior basins where dominant plants are coarse grasses. Scattered trees, such as palms, are common, but few shrubs are listed.

Gentry (1942) uses the term "short tree forest" for part of the tropical deciduous forest in western Mexico. In his publication Rio Mayo Plants, he lists 209 shrubs found in the Rio Mayo Basin, which include thorn forest, short tree forest, oak forest and pine forest. Most of these shrubs are found in the thorn forest and short tree forest.

The Arid Tropical Shrub, very limited in extent with a typical cover of leguminous trees and bluestem bunchgrass, includes shrubs along with several succulent species.

Identification of North American shrubs

In addition to the large number of general taxonomic works covering various regional, State, and local floras, there are some noteworthy publications which are oriented toward woody plants. Among those with a wide geographical coverage are the two very useful books: *Native Woody Plants of the United States, their Erosion-Control and Wildlife Values* (Van Dersal 1938) and *Ornamental American Shrubs* (Van Dersal 1942). Other good sources are: *Manual of Cultivated Trees and Shrubs Hardy in North America Exclusive of the Subtropical and Warmer Temperate Regions* (Rehder 1940), and the *Woody-plant Seed Manual* (USDA Forest Service 1948). *The Shrub Identification Book* (Symonds 1963) and *The Book of Shrubs* (Grimm 1957) are two well-illustrated publications covering mostly shrubs of northern and eastern North America.

Publications having considerable information on shrubs include *Standardized Plant Names* (American Joint Committee on Horticultural Nomenclature 1942), *The Standard Cyclopedia of Horticulture* (Bailey 1935), *Native American Forage Plants* (Sampson 1924), and *Important Western Browse Plants* (Dayton 1931).

Useful publications relating to the identification of shrubs in northern and eastern North America include *The Shrubs of Northeastern America* (Newhall 1893), *Vermont Shrubs and Woody Vines* (Jones and Rand 1909), *Trees and Shrubs of Minnesota* (Rosendahl and Butters 1928), *Trees and Shrubs of New Hampshire* (Foster 1931), and the revision and enlargement of a 1903 publication entitled *Our Northern Shrubs and How to Identify Them* (Keeler 1969). The southeastern United States is well covered by *Trees and Shrubs for the Southeast* (Wigginton 1963). These publications also provide information on the shrubs of the midwestern States. A more inclusive treatment is found in *Shrubs of Indiana* (Deam 1932). Although geographically it would seem to belong in the grassland region, *Trees, Shrubs, and Woody Vines in Kansas* (Stephens 1969) includes many midwestern shrubs.

There are few publications devoted to shrubs in the Central Grassland. Stephens (1969) gives information on shrubs of the central prairie region. The comprehensive publication *Trees, Shrubs and Woody Vines of the Southwest* (Vines 1960) provides good coverage for the southern portion of the grassland in the United States. This is augmented by *Trees and Shrubs of New Mexico* (Wooton 1913). In the Northern United States, *The Shrubs and Climbing Vines of South Dakota* (Hansen 1931) and *The Shrubs of Wyoming* (Nelson 1902) help fill in the gap; *A Guide to the Woody Plants of Colorado* (Kelly 1970) covers the western edge of the grassland. This very useful guide also provides a great deal of information on shrubs of the Rocky Mountain area.

The Northern and Central Rocky Mountain region is covered by several good publications including *Trees and Shrubs of the Rocky Mountain Region, with Keys and Descriptions for their Identification* (Longyear 1927), *Northern Rocky Mountain Trees and Shrubs* (Kirkwood 1930), and *Guide to the Woody Plants of the Mountain States* (Treshow and others 1970). For the warm deserts of the southwestern United States, *Vegetation and Flora of the Sonoran Desert* (Shreve and Wiggins 1964) is excellent for the area covered. Other pertinent publications include: *Trees, Shrubs and Woody Vines of the Southwest* (Vines 1960) and *The Trees and Shrubs of the Southwestern Deserts* (Benson and Darrow 1954). For Mexico, the classical publication is *Trees and Shrubs of Mexico* (Standley 1920-1926).

The Pacific Coast is well covered by manuals, but the publications relating to shrubs tend to be of a popular nature or largely concerned with nonnative ornamentals. Three of value are: *The Trees and Shrubs of Western Oregon* (Benson 1930), *Ornamental Shrubs of California* (Enari 1962), and *Native Shrubs of Southern California* (Raven 1966).

Useful wildland shrubs

The economic attributes of shrubs are covered in the following publications: *Plants Useful to Man* (Robbins and Ramaley 1933), *Useful Wild Plants of the United States and Canada* (Saunders 1934), *Plantas Utiles de la Flora Mexicana* (Martinez 1959), and *Dictionary of Economic Plants* (Uphof 1968). For arid lands in particular, a book entitled *Food, Fiber, and the Arid Lands* (McGinnies and others 1971) is useful.

The following publications place emphasis on food plants, especially those used by native American races: *Uncultivated Native Plants Used as Sources of Food* (Castetter 1935), *Food Plants of North American Indians* (Yanovsky 1936), *Edible Wild Plants of Eastern North America* (Fernald and Kinsey 1943), and *Edible Native Plants of the Rocky Mountains* (Harrington 1967).

Some special references on uses of arid lands plants include: *The Mesquite Tree, Its Products and Uses* (Forbes 1895), *An Economic Study of Acacias* (Shinn 1913), *Saltbushes and Their Allies in the United States* (Bidwell and Wooton 1925), *A Rubber Plant Survey of Western North America* (Hall and Goodspeed 1919), *Rubber Content of Native Plants of the Southwestern Desert* (Buehrer and Benson 1945), *Guayule, an American Source of Rubber* (Taylor 1951), and *Simmondsia or Jojoba, a Problem in Economic Botany* (Mirov 1952).

According to Dayton (1931), the browse crop on western ranges in the United States is largely produced by 24 plant families and 60 genera. At least six families and 17 genera include poisonous plants.

Nine families are of outstanding importance and interest. These are the rose family (Rosaceae), including the apple (Malaceae), and almond (Amygdalaceae) families; the legume family (Leguminosae), including the mimosa (Mimosaceae), cassia (Caesalpinaceae), and ratany (Krameriaceae), aster family (Compositae), goosefoot family (Chenopodiaceae), buckthorn family (Rhamnaceae), oak family (Fagaceae), honeysuckle family (Caprifoliaceae), willow family (Salicaceae), and heath family (Ericaceae).

The rose group (Rosaceae) is, with the possible exception of the composites (Compositae), the most widely developed shrub family in the West and is perhaps the most important as range browse. It contains a considerable number of excellent forage shrub species--mountainmahogany (*Cercocarpus*), bitterbrush (*Purshia*), cliffrose (*Cowania*), Apache plume (*Fallugia*), and rose (*Rosa*).

The apple and peach families, often treated as subfamilies of the rose family, contain a considerable number of browse genera. These include: serviceberry (*Amelanchier*); mountain-ash (*Sorbus*); plums, cherries, and chokecherries (*Prunus* spp.); hawthorns (*Crataegus*); and the squawapple (*Peraphyllum*) of the Great Basin Region.

The bean or legume family (Fabaceae or Leguminosae), in a restricted sense, furnishes little or no browse on western ranges; on the other hand, it does produce several toxic woody genera, such as locust (*Robinia*), mescalbean (*Sophora*), broom (*Cytisus*), and peabush (*Parosela*).

Closely allied to the pea family, especially the older ones, are three taxa considered as subfamilies by many botanists: mimosa or sensitive plant (Mimosaceae); cassia or senna (Caesalpinaceae), and ratany (Krameriaceae), all of which are of particular importance in the Southwest. To the mimosa family belong catclaw or acacia (*Acacia*), false-mesquite (*Calliandra*), sensitive plant (*Mimosa*), and mesquite (*Prosopis*).

The largest of all plant families, the Compositae, does not include many palatable browse species, aside from the large sagebrush genus (*Artemisia*). However, some of

the palatable species do have wide distribution and abundance and the large percentage of the range occupied by them counteracts in large measure their more limited palatability per plant.

One of the most valuable groups of western browse plants are members of the goosefoot family (Chenopodiaceae), especially in the plains and Great Basin regions. Here are found such shrubs as the saltbushes and shadscales (*Atriplex*), winterfat or white sage (*Eurotia*), greasewood (*Sarcobatus*), and hopsage (*Grayia*).

The buckthorn family (Rhamnaceae) is of grazing interest almost solely because of one very important genus (*Ceanothus*). One of the California species, bluebrush (*Ceanothus integerrimus*), is the most important browse plant.

The oak family (Fagaceae) is of western forage significance primarily because of the vast stretches of shrubby or low-arborescent oaks that form distinct types on numerous western ranges.

The honeysuckle family (Caprifoliaceae) provides a large number of woody genera that are more or less grazed; perhaps the most important of which are the snowberries and coralberries (*Symphoricarpos* spp.), and the elders (*Sambucus* spp.).

The heath family (Ericaceae) is a large and important group of shrubs and trees. It is confined, however, to acid soils with grazing interest being primarily in the genera that are poisonous to livestock, such as the azaleas, rhododendrons, menziesias, Labrador teas, staggerbushes, and various other toxic genera popularly and promiscuously termed "laurels."

Other plant groups that furnish shrubs of forage value on some western ranges include the jointfir family (Gnetaceae) to which the jointfirs or Mormon-teas (*Ephedra*) belong; buckwheat family (Buxaceae) on account of the important southwestern shrub jojoba (*Simmondsia*); the cashew family (Anacardiaceae) because of the fair palatability of some sumacs (*Rhus* spp.); the maples (*Acer* spp.); the shrubby bushmints (*Hyptis*) and sages (*Salvia*) of the mint family (Menthaceae) occurring in California, the Great Basin, and the Southwest.

Many North American shrubs are used as ornamentals. From the eastern part, such shrubs as dogwoods, hawthorns, bayberries, plums, sassafras, hydrangeas, and wild cherries have been domesticated. The Appalachian region has been especially productive of fine flowering shrubs including the rhododendrons, azaleas, crabapples, viburnums, hollies, buckeyes, and others. The grasslands have given us buffaloberries, currants, wild roses, amorphas, silverberries, and others. From the western mountains come the manzanitas, the mahonias, ceanothus, buckthorns, cherries, mockoranges, and oceansprays. The Great Basin is the home of the golden rabbitbush and the sagebrushes, and the Southwest the home of algeritas, flowering almonds, creosote bush, smoketree, evergreen sumacs, and last but by far not least, the great variety of flowering shrubs native to California.

Van Dersal's *Ornamental American Shrubs* (1942) lists the 10 best ornamental shrubs for the Northeast, Southeast, Northwest, Southwest, and California. His summary of the 10 best ornamental shrubs for the United States follows:

1. *Rhododendron calendulaceum*, the flame azalea, chosen as the finest ornamental shrub in the United States because of the brilliant intensity of its flower color and its gorgeous display in bloom.

2. *Fremontia mexicana*, the San Diego fremontia, chosen because of its beauty and profusion of bloom, shapely habit, and loveliness of individual flowers.

3. *Sophora secundiflora*, the mescalbean sophora, chosen for its first-class foliage, showiness in bloom, and exquisite fragrance and color of flower.

4. *Kalmia latifolia*, the mountain-laurel kalmia, chosen for its elegance in full bloom, excellence of evergreen foliage, and beautiful symmetry of flowerbud.

5. *Rubus deliciosus*, the boulder raspberry, chosen because of its remarkably showy bloom, excellent flowers, foliage, and habit.

6. *Ceanothus impressus*, the Santa Barbara ceanothus, chosen for the intense blue of its flowers, loveliness in bloom, unusual foliage, and fountain-like habit.

7. *Chionanthus virginica*, the white fringetree, chosen for the laciness and profusion of its flowers, the attractiveness of its fruits, and loveliness of perfume.

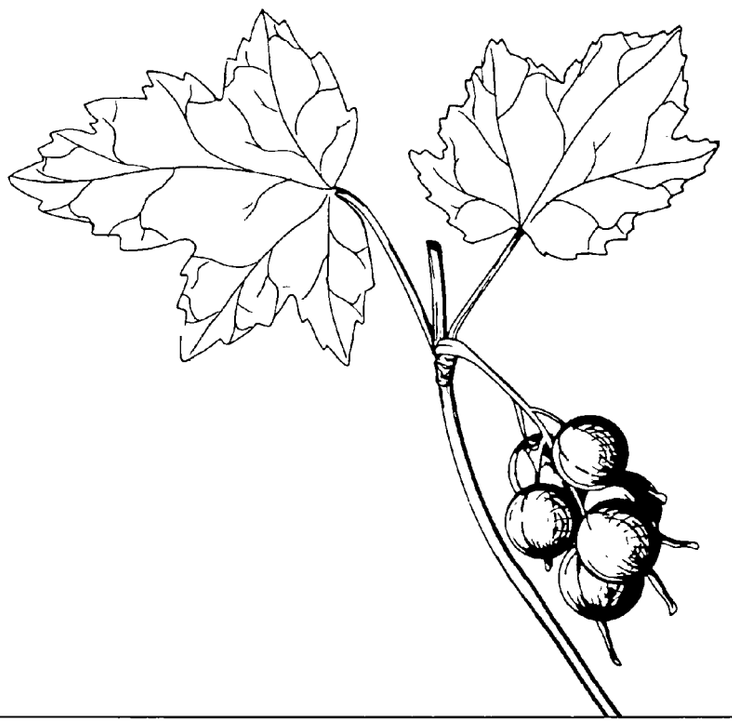
8. *Stewartia ovata* var. *grandiflora*, the mountain stewartia, chosen for the beauty of its foliage, the large size and elegance of its flowers, and beautiful autumn color.

9. *Ilex vomitoria*, the yaupon, chosen for its remarkable production of brilliant crimson fruits, good habit, and fine evergreen foliage.

10. *Viburnum trilobum*, the cranberrybush, chosen for its beauty of bloom, excellent foliage, showiness of fruit, and fine autumn color.

Section II.

Present and Possible Uses of Shrubs



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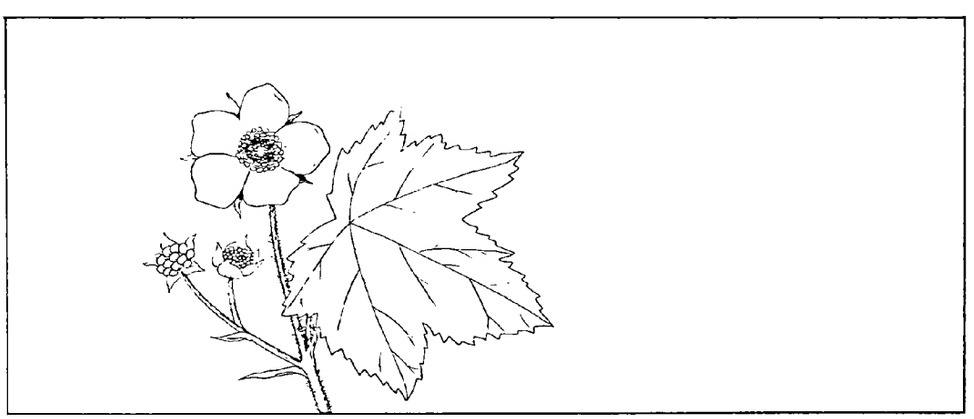

Browse and cover for wildlife

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The importance of shrubs to wildlife is widely recognized. Yeager (1961) pointed out that nearly half of the 369 mammal species and 58 percent of 714 birds indigenous to North America are associated with woody cover, of which shrubs are an important component. The dependence of some wildlife species on specific shrubs is suggested by such common names as rabbitbrush (*Chrysothamnus*), sagegrouse (*Centrocercus urophasianus*), willow grouse (*Lagopus lagopus*), and bearberry (*Arctostaphylos uva-ursi*).

Approximately 1,000 species of shrubs, semishrubs, and woody vines from 225 genera and 68 families grow within the National Forests of the contiguous United States alone (Dayton 1931). In the semiarid Western United States, several predominantly shrub types cover extensive areas. Also, in the forest understory and in prairies and savannas, their presence leads to niche diversification, which permits a greater number of individuals and species to occupy the habitat. Ovington (1964) determined that a Minnesota savanna supporting trees, shrubs, forbs, and grasses produced significantly more plant material annually above ground per unit area than a nearby grassland. If animals are present that can effectively use the plant material, secondary productivity of the savanna should also exceed that of the grassland.

Besides providing food, shrubs supply necessary cover where wildlife can escape predators, rear young, and ward off the elements. This paper reviews some ways in which shrubs contribute to the welfare of wildlife, and suggests how desirable shrubs can be fostered to maintain and improve wildlife habitat.

Shrubs as food

Nearly every shrub provides food for one or more species of wildlife. Martin and others (1951) reported use of shrubs as food by 117 wildlife species indigenous to the United States. Of 76 plant genera most commonly used, nearly one-fourth are shrubs. Following are shrubs widely used for food and the numbers of wildlife species known to use them:

Prunus (chokecherry, plum)	81	*Salix* (willow)	25
Rubus (blackberry, raspberry)	97	*Arctostaphylos* (manzanita, bearberry)	19
Cornus (dogwood)	64	*Alnus* (alder)	16
Toxicodendron (poison ivy)	61	*Symphoricarpos* (snowberry)	27
Opuntia (prickly pear)	44	*Ribes* (currant)	32
Vaccinium (blueberry)	63	*Atriplex* (saltbush)	22
Prosopis (mesquite)	24	*Smilax* (greenbriar)	33
Sambucus (elderberry)	79	*Rhus* (sumac)	50
Amelanchier (serviceberry)	58	*Artemisia* (sagebrush)	22

These genera include a minimum of 625 plant species within the continental United States and upwards of 1,800 worldwide.

Selective feeding

Individual food preferences vary (Smith and Hubbard 1954), but many wildlife species show seasonal preferences for different shrub species as well as shrub parts--foliage, twigs, buds, bark, flowers, nectar, fruit, seeds, and roots. Some shrubs, particularly fleshy cacti, are also utilized for their water content in semiarid regions. Shrubs become increasingly important to herbivores during seasons of plant dormancy--winter in the arctic and temperate regions and the dry season in the deserts and tropics. The shift to shrubs is largely motivated by nutritional requirements, but availability is also influential, particularly when the ground is snow-covered. In the dry tropics, many woody plants leaf out a month or two before the rains, at a time when high quality food is scarce (Lawton 1968). These woody plants can leaf out early because their roots are deeper, often extending to the water table. The content of protein, calcium, and phosphorus is generally greater in shrubs at this time than in senescent forbs and grass (Watkins 1937; Stoddart and Smith 1955). Species and plant parts vary considerably in nutritive value. Dougall and others (1964) found that legume browse in East Africa contained more protein than nonlegume browse. Fruits and seeds of shrubs are often concentrated sources of starch, sugar, protein, or fat, and are particularly sought by birds, rodents, and many of the larger mammals. Leaves, buds, flowers, and inner bark are usually more nutritious than twigs, because they contain less digestible cellulose and lignin (Lay 1969; Blair and Epps 1967). Bailey (1967) found progressively lower proportions of protein in flower buds, vegetative buds, terminal 1-inch twig tips, and the remaining current twig growth of witch-hobble (*Viburnum alnifolium*). Evergreen shrubs are usually more nutritious and palatable during dormancy than deciduous ones because leaves are generally more digestible than twigs.

Selective feeding by wildlife is explained partly by differences in digestible nutrients since the food taken generally contains more nutrients than plant parts that are left. For deer (*Odecoileus*), Longhurst and others (1968) found positive correlation between shrub acceptance and digestibility. However, other factors also influence choice. Many otherwise palatable shrubs are protected by thorns. Some shrubs are very nutritious but not very palatable. Shrubs containing a variety of alcohols and aromatic oils are less palatable than some others; but the reason--whether taste or some subsequent adverse effects on the digestive organs--is not always clear. Highly aromatic plants are poorly accepted, apparently in part because they inhibit certain digestive bacteria. The volatile oils of sagebrush adversely affect the rumen bacteria of mule deer (*Odocoileus hemionus*) (Dietz and others 1962; Nagy and others 1964). I have observed that mule deer in Utah normally do not feed on elderberry (*Sambucus*) or chokecherry (*Prunus*) until about the time of the first frost; then they eat this foliage avidly. Acceptance seems to result from chemical changes. Young chokecherry shoots cause prussic acid poisoning in livestock, but the danger lessens as the leaves mature (Dayton 1931).

Of interest in big game nutrition is the relative value of two browses--balsam fir (*Abies balsamea*) and white cedar (*Thuja occidentalis*)--to two cervids--white-tailed deer (*O. virginiana*) and moose (*Alces americana*). Balsam fir is considered fair to good winter browse for moose but starvation fare for deer, whereas the reverse is true for white cedar (Davenport 1939; Ullrey and others 1967). The explanation must lie in the differences in efficiency of the digestive organisms in the two species.

Burned areas commonly produce shrubs unusually rich in protein and eagerly sought by herbivores (Einarsen 1946; Swank 1956). Open-grown shrubs are commonly preferred to understory shrubs. Artifical fertilization of nitrogen-deficient soils can increase the nutritive value of the forage and its palatability to wildlife (Miller

1968), and the nature of the base rock can also influence soil fertility and plant palatability (Jenkins and Watson 1970).

Use by big game

Several studies have stressed the importance of browse and shrub diversity in providing game animals with a balanced diet. In the southern United States, where deer rely heavily upon fruits and mast from woody plants, variety is necessary because many plants are erratic producers (Lay 1969; Goodrum and Reid 1958). Dougall and others (1964), in extensive chemical analyses of East African forage plants, demonstrated the variability of nutrients, seasonally and by species.

Loss of variety caused by overuse and destruction of the preferred forage species can result in big game herd losses. Severinghaus (1951) reported a drop in fawn production from 1.9 per adult white-tailed doe during the first 2 years in a New York enclosure to only 0.4 after overuse of most of the 44 browse species. Similarly, an unhunted mule deer herd on 2,300-acre Wildhorse Island in Montana declined from a peak of 500 in 1955 (Woodgerd 1964) to only 50 in 1970 (Ford 1971); the primary cause was extreme overbrowsing. Goodrum and Reid (1958) found no surviving white-tailed fawns in a Mississippi enclosure for 3 years following overuse of five or six browse species of some 25 available. Winter losses of mule deer in Utah were inversely related to available shrub browse and particularly that of the preferred species (Robinette and others 1952). One area, no longer supporting any preferred browse, suffered a 40 percent herd loss during a severe winter, compared with only 10 percent for an area that had an adequate supply.

Martinka (1967) observed similar losses of pronghorns (*Antilocapra americana*) in Montana. During a severe winter, losses were heavy in an area where sagebrush was scarce, but light to moderate where it was available in adequate quantities. Subsequent fawn crops in the two areas were 39 and 90 fawns per 100 does, respectively. These results seem explained by the findings of Longhurst and others (1968) that deer preference for forage was positively correlated with digestibility.

Verme's (1962) feeding trials in Michigan demonstrated the importance of overwinter nutrition of white-tailed does to early postnatal fawn mortality. The extremes were 94 percent mortality for offspring from does on the poorest diet and only 6-7 percent for the best. Studies by Julander and others (1961) revealed the value of preferred forage, of which shrubs are an important part, in the summer diet of mule deer. Herds were compared in two areas; preferred browse was about 10 times more abundant in one than in the other. Fall fawn weights on the good range were about 50 percent greater than on the poor range, and the fetal rate for yearling does on the good range was more than double than on the poor range.

Recent studies in East Africa demonstrate the importance of browse, including a variety of shrubs, to elephants (*Loxodonta africana*), possibly the most versatile feeders among the herbivores. A tame animal, followed for 11 hours during one day in Tsavo National Park, was observed to feed on 64 plant species (Dougall and Sheldrick 1964). Even though the grasses were still green, 20 of the species of plants eaten were shrubs or semishrubs. Elephants used 88 percent of the 255 woody species found in the Kibale Forest Reserve in Uganda (Wing and Buss 1970). Elephants prefer herbaceous forage while it is green but turn to browse during the dry season. Adult elephants can survive the dry season on a predominantly grass diet (Buss 1961), but their physical condition and productivity suffer (Laws and Parker 1967). In a National Park where the woody cover has largely been eliminated during the past 20 years through a combination of elephant use and fires, the elephant calving interval has more than doubled (from 4 years or less to 8-9 years) and the age of female puberty has increased from about 12 years in 1947 to 18 years in 1965 (Laws 1968). These factors, plus heavy calf mortality, led to a 12 percent herd decline between 1958 and 1963 (Laws 1968).

Results of increase in availability of browse demonstrate its value to big game. Extensive forest fires, with the increased shrubby growth that follows, have been credited with substantial increases of moose on Alaska's Kenai Peninsula (Spencer and Hakala 1964) and Michigan's Isle Royale (Aldous and Krefting 1946) and of elk in Idaho's Selway Wilderness Area (Parsell 1938). Swank (1956) in Arizona, and Taber and Dasmann (1958) in California reported deer densities averaging four to five times higher on burns than on adjacent unburned chaparral. All these studies showed that burns produced forage that was readily available and more nutritious than before. Bear populations increase on burned areas because of the increase of fruits and berries (Costello 1957). Logging, by opening up the forest canopy, also increases available browse and deer densities (Patton and McGinnes 1964). In some locales, overuse by cattle has reduced and produced a subsequent increase of forbs and shrubs. All these habitat improvements, together with stricter law enforcement and predator control, have collectively accounted for phenomenal increases in deer throughout the United States from 1920 to 1950 (Leopold 1950).

The influence of vegetational diversity on variety of wildlife species was reported by Dowsett (1966), who found 21 big game species in the woodland portion of his study area in Kafue National Park, Zambia, compared with only 14 in grassland, nine in dense thicket, and six in forest. The woodland, with its open tree growth, permitted the greatest variety of available plant species and consequently of mammals. Lamprey (1963) found the greatest variety of big game species and the highest biomass among ecotones in his study in Tanzania.

Use by other mammals

Many mammals other than big game rely upon shrubs for food. Even some mammals whose foods are largely of animal origin eat fleshy fruits from shrubs in season. These include foxes, coyotes, jackals, civets, mongooses, raccoons, ring-tailed cats, skunks, armadillos, opossums, and others. Certain bats consume fruits and juices (Bourlière 1964; Cockrum 1962). Many other mammals, especially primates and numerous rodents, are largely vegetarian; so shrubs supply part of their diet (Smithers 1966).

Vegetarian smaller animals, like big game, often seek herbaceous food during the growing season, showing a trend toward woody plants during fall and winter. During fall and winter, porcupine and beaver feed almost exclusively on the inner bark of woody plants. Lagomorphs feed mostly on twigs or evergreen leaves of woody plants; however, during deep snows, they rely upon bark as well. Most of the tree squirrels and mice native to the United States are seed eaters during this period. However, during critical winters or population highs, mice may turn to bark. Spencer (1958) recorded serious barking and girdling of sagebrush, bitterbrush (*Purshia*), chokecherry, mountainmahogany (*Cercocarpus*), rose, and currants by mice (*Microtus*, *Lagurus*, and *Clethrionomys*) during a mouse irruption in Oregon.

Availability of preferred foods is probably as important for the smaller animals as for big game. A New Mexico study (Huey 1956) showed that a group of beaver on an aspen diet produced litters double those of a group feeding on willow. Independent studies (Hall 1960; Panfil 1960) bear out that North American and European beaver prefer aspen to willow. Like big game, snowshoe hares (*Lepus americanus*) and several small rodents (*Peromyscus*, *Eutamias*, and *Microtus*) respond favorably to burning and timber cutting (Gashwiler 1970).

Use by birds

Birds have nearly as diverse feeding habits and use of shrubs as mammals. Some species feed largely on leaves and buds, some are nectar feeders, but most use fruits and seeds.

Martin and others (1951) report that ducks make limited use of the seed and fruits of eight shrub species; but the gallinaceous birds depend much more upon shrubs. Grouse, in particular, are heavy users of the leaves, buds, flowers, and fruits of many shrubs. The leaves and shoots of heather (*Calluna vulgaris*) are the most important yearlong food of rock ptarmigan (*Lagopus mutus*) (Moss 1968), of red or willow grouse (*L. lagopus*) in Scotland (Jenkins and Watson 1970), and of black grouse (*Lyrurus tetrix*) in Denmark (Joensen 1967). Hoglund (1970) reported that willow grouse in Sweden used little heather, but preferred various species of *Vaccinium*, *Empetrum*, and *Andromeda* during the snowfree period, and buds and catkins of *Betula* and *Salix* in winter. The summer foods of spruce grouse (*Canachites canadensis*) in Alaska (Ellison 1966) are similar to those of willow grouse in Sweden; they prefer berries, buds, and leaves of *Vaccinium* and *Empetrum*, but they consume minor amounts of *Arctostaphylos* berries, rose hips, and other fruits. A study of blue grouse in Washington (Boag 1963) suggested that population declines when preferred fall foods are scarce. Grouse in the warmer climates usually have a more varied diet in response to a greater diversity of plant species. Korschgen (1966) found that ruffed grouse (*Bonasa umbellus*) in Missouri had taken food from 111 species or groups of plants and that 45 percent of their yearlong food was supplied by understory trees, shrubs, vines, and brambles. Sagegrouse (*Centrocercus urophasianus*) of the Western United States, however, relies heavily upon the leaves, shoots, and seed stalks of sagebrush, especially during fall and winter (Martin and others 1951). Birds such as grouse that subsist at least part of the year on fibrous plant material are aided in digestion by bacteria, particularly in the caecum (Suomalainen and Arhimo 1945).

Most nongame birds that utilize shrubs for food take fruits or seeds. At least 12 of the 18 important shrub genera listed earlier produce fruits that are heavily used by songbirds. A notable exception to fruit-or-seed feeders among the songbirds are the nectar feeders, especially common in the tropics and represented worldwide by 650 species. Shrub flowers are much used for their nectar.

Shrubs as cover

Use by mammals

The value of shrubs as cover for mammals has not been studied extensively. Woody cover is unquestionably important to many mammals as shade during hot weather (Ables and Ables 1969). It is also important during winter in colder areas because it moderates temperature and wind velocity (Loveless 1967).

A windbreak of trees and shrubs in an otherwise treeless area of South Dakota affected the winter distribution of white-footed and harvest mice (*Reithrodontomys*) on the leeward side (Vose and Dunlap 1968). There were significantly more mice 37 meters from the windbreak than at 74 and 111 meters. Less wind at the closest distance accounted for deeper snow and heavier litter, which attracted the mice because of the protection they provided against predators and weather. Loveless (1967) noted that winds stronger than 25 m.p.h. and temperatures lower than 15° F. caused mule deer in Colorado to seek cover.

Many mammals use shrub cover to hide or escape from predators, and some predators use shrubs for concealment while stalking prey. Cottontails rarely venture far from brushpiles or dense patches of shrubs during winter. Allen (1939) and Lord (1963) reported brushy areas as having the highest cottontail populations in Illinois. Brush rabbits (*Sylvilagus bachmani*) seem even more dependent upon brush for cover. Their average center of activity was 40 feet inside the edge of brush in California, and they seldom would venture more than 70 feet into the open (Connell 1954). Deer normally feed close to cover. Reynolds (1964a) discovered from pellet group counts that prevalence of deer and elk increased with shrub density in southwestern New Mexico. The association appeared to be related to both the food and cover provided by shrubs. Deer in the semiarid Western United States commonly feed not more than one-fourth mile

from cover (Leopold and others 1951; Reynolds 1964b). Loveless (1967) found that during the winter, mule deer in Colorado most often used shrub-covered slopes close to timber cover. Preferred calving grounds for elk in Montana were sagebrush openings within 100 yards of timber (Johnson 1951). Most big game ungulates with nonprecocious young utilize cover, often shrubs, for concealing their young for 2 to 3 weeks or more following birth. Mule deer in Utah prefer sagebrush and snowberry 2 to 3 feet high and near taller cover for the does. Even African plains animals, such as Thomson's and Grant's gazelles (*Gazella thomsonii* and *G. granti*), use low shrubs or semishrubs for concealing their young lambs.

Use by birds

Birds require cover for shade, for protection against the elements and predators, for loafing or roosting, and during the breeding season for singing perches and nesting sites (Johnston 1970). Shrubs fulfill these needs for many birds. Increased stratification of the vegetation usually produces higher densities of nesting birds. A study on the grounds of a field research station in Virginia revealed 22 species of breeding birds at a density of 800 pairs per 100 acres compared with only 16 species and 190 pairs per 100 acres in the adjacent deciduous forest (Johnston 1970). The differences were attributed to clearings on the station grounds, together with shrub plantings, which created variable vegetative strata and increased habitable niches. Hooper and Crawford (1969) reported that the understory in forest types was the most important factor in breeding densities of nongame birds in the southeastern United States.

A great many birds nest in or under shrubs. Within the United States and Canada, at least 181 species rely wholly or in part upon shrubs as nesting cover (Peterson 1961). Austin (1970) found that foliage volume was an important factor in the selection of shrub nesting sites in a desert riparian type; the more compressed the foliage, the more favorable, because of the added protection from predators and weather. In the oak-juniper woodland in southern Arizona, each breeding pair of birds required an average of 73,000 ft.^{3} of foliage (Balda 1969). Some bird species were restricted by a particular plant species or life form, whereas others used a particular height in the canopy regardless of plant species. Karr (1968) found a close relation between variety of breeding birds and foliage height, diversity, and percent of vegetative cover. He made the following observations in strip-mined coal areas of Illinois for various successional stages in the vegetation:

	Bare	*Early shrub*	*Late shrub*	*Forest*
Pairs of breeding birds per 100 acres	28	341	375	489
Number of bird species	5	18	32	32

Improving wildlife habitat with shrubs

Research has repeatedly confirmed the value of vegetative type interspersion or "edge" to wildlife. Wildlife managers can increase type interspersion in many ways.

Climax forests generally harbor few wildlife species, and these have small populations. A varied wildlife habitat within forest types, which cover about one-third of the United States, is largely maintained by fire, plant disease, or timber cutting. Most American forests are now under some type of rotational cutting that assures a continuing supply of the herbs, tree sprouts, and shrubs essential to a varied fauna. In some areas that have high recreational and timber values, management plans are closely coordinated to produce maximum yields of both game and timber.

In parks, game refuges, or areas that have low timber values, habitat improvement undertaken explicitly for wildlife may be justified. An excellent example is the action taken to encourage a rare songbird, Kirtland's warbler (*Dendroica kirtlandi*). For nesting, it requires relatively open stands of young (8-20 years) jack pine (*Pinus banksiana*) in a limited area in Michigan. One-square-mile blocks of mature timber are to be burned periodically by concerned agencies to insure continuing nesting habitat (Line 1964). Berner and Gysel (1969) have recommended a 10 percent removal of aspen in small openings to improve production of ruffed grouse in Michigan. Sharp (1963) obtained substantial increases in populations of ruffed grouse in pole-size timber in Pennsylvania by creating numerous 1/4- to 1-acre openings. Tall shrub cover is an element in the selection of drumming logs by male ruffed grouse (Palmer 1963), and openings with an interspersion of shrubs, herbs, and bare ground are needed as breeding habitat for blue grouse in Canada (Bendell and Elliott 1966). Openings of 5 acres or less in aspen were recommended by McCaffery and Creed (1969) for improving deer habitat in Wisconsin. These openings also favor hares and many species of songbirds and rodents. Such small openings may be achieved by cutting, girdling, or bulldozing the trees. Krefting and Hansen (1969) achieved a partial clearing of scrub timber and reduction of little-used hazel (*Corylus*) in Minnesota by an aerial spraying of 2,4-D, which increased the volume of preferred shrubs that deer use.

Leopold and others (1963) proposed the use of fire to maintain essential wildlife habitat in some United States parks, and the National Park Service now uses prescribed burning in some areas and permits naturally occurring fires to run their course in others (Houston 1970). Controlled burning along with food and cover plantings, including shrubs, has long been a quail management tool in pine woods of the southern United States (Rosene 1969).

Dwarf trees, such as pinyon pine and juniper, in the southwestern United States have become so dense in many areas as to crowd out shrubs valuable for wintering big game. Reynolds (1964b) found that shrubs and big game use declined when the density of junipers and pinyons exceeded 150 to 200 per acre in New Mexico. Several State game departments and federal agencies have begun range improvement programs to eradicate these trees from strips or blocks and seed the areas to grass, forbs, and shrubs. Following removal of pinyon and juniper on the Kaibab National Forest in Arizona, Reynolds (1964b) reported increases in cliffrose (*Cowania mexicana*), sagebrush, and herbs, and in use by deer.

Shrub growth is often too dense for optimum use by wildlife. Openings in dense mature chaparral created by fire or mechanical means have been helpful to deer, quail, rabbits, and doves (Swank 1956). Hendricks (1968) reported browse production of 2,000 lb. per acre on a California burn compared with a less nutritious 50 lb. in mature brush. Burning likewise appears to improve the habitat of red grouse in Scotland (Jenkins and Watson 1970). Numerous small burns in the heather increased the breeding stock by 50 percent over that of untreated areas. Burning increased the protein level of the heather and maintained optimum nesting cover, which should not exceed 1 foot in height.

Protection of shrubs from overuse by herbivores or from eradication during rehabilitation of livestock ranges can often maintain wildlife habitat. This is especially true on critical big game winter ranges where sagebrush, willows, and other shrubs are being eradicated and the areas seeded to grass for livestock. Reduction of shrubs by use of phytocides appears to have been detrimental to sage grouse (Klebenow 1970) and prairie chickens (Jackson and DeArment 1963), and phreatophyte control has adversely affected dove nesting in the Southwest (Gallizioli 1961). State game departments and federal agencies are increasing their efforts to preserve adequate areas of these critical brushlands on public lands to assure huntable game populations. Holding big game to the range carrying capacity by hunting is of course another practical means of preserving important shrubs.

In many areas, though, it may be necessary to reseed or plant shrubs. This is particularly true for agricultural areas and on depleted big game ranges. Many indigenous and exotic shrubs have been recommended for wildlife habitat plantings (Rosene 1969; Wandell 1948; and Plummer and others 1968). Quail, cottontails, and songbirds seem to have benefited especially by shrub plantings (Burger and Linduska 1967). Rehabilitation of big game ranges is usually especially difficult because of the need for protecting seedlings during establishment. However, experience in Utah has demonstrated the feasibility of this procedure on an operational scale (Plummer and others 1968).

Low-maintenance landscaping

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Description and uses

Low-maintenance shrubs are valuable for such special purposes as roadside plantings, erosion control, range use, traffic guidance, and wildlife protection. The term "low-maintenance" must be applied with respect to a particular area. Climate, soil, topography, and other conditions determine whether a shrub is in the "low-maintenance" category. In heavy snow country, a low-maintenance shrub may be one that successfully resists salt damage along roadsides, or one that can withstand heavy snow, such as manzanita (*Arctostaphylos patula* Greene). In warm moist or cool moist climates, many native or introduced shrubs growing without assistance from man may be considered as low maintenance shrubs. A particular shrub may be classed as "low-maintenance" on level, stable ground, but not on highly erosive soils on sloping terrain. In arid or cold climates, low-maintenance shrubs are likely to be native and well adapted to local temperature ranges, moisture, salinity, or soil conditions. For roadside plantings, such shrubs may be those that survive in the area and do not attract wildlife and other browsing animals. In arid climates, "low-maintenance" usually implies the ability to live and grow under conditions of low soil moisture, high daytime temperatures, and, often, salt-affected soils. Conversely, in humid climates a desirable low-maintenance shrub may be one that does not grow so rapidly that it damages pavement, does not cause allergies, or does not require frequent pruning. "Low-maintenance" for a specific area could also mean resistance to attack by a particular insect or disease pest or the ability to withstand one extremely cold or dry year in twenty.

Thus, a low-maintenance shrub is one that can grow well and reproduce at a given location in a particular climate with little or no treatment by man, and remain free of serious disease or insect pests. Some authorities might wish to omit from this definition the ability of the shrub to reproduce, but for many situations this characteristic is essential. Low-maintenance shrubs for wildlands are very different from the cultivated shrubs used ornamentally or in municipal plantings, where every protection is provided against the vagaries of climate, attacks by insects and pathogens, and other threats, and plants are given fertilizer, water, pruning, and other special care.

A broad survey of the literature on low-maintenance shrubs in the Western United States suggests that their major use is for highway plantings and for prevention or control of soil erosion. However, shrubs have not been used extensively for these special purposes because wildland grasses are easy to plant and maintain. Shrub species that have been tried in plantings along highways in Arizona include fourwing saltbush (Chamizo) (*Atriplex canescens*), *Baccharis* sp., creosotebush (*Larrea divaricata*) and rough menodora (*Menodora scabra*) (U. Ariz. Agr. Exp. Sta. 1964; Charles 1963; Earley and Hogan 1963). In California, the rose (*Rosa wichuraiana*) and grape (*Vitis capensis*)

were not vigorous enough to compete with the weeds; other species tried were too short-lived or required too much water. Plantings of low succulent herbs such as *Mesembryantheum croceum* have been successful on poor soils, and so have vines (Bowers 1950; Horton 1949; Mathias and others 1961). In New Mexico, sumac (*Rhus trilobata, R. glabra*), desert almond (*Prunus fasciculata*), and *Yucca* sp. have proved to be low-maintenance plants for some habitats. Astrup (1951) and Martel (1964) have developed lists of plants for erosion control in the humid portions of Oregon, but little horticultural information is available about shrubs suitable for planting in the arid areas of the State. In Wyoming, the native sagebrush (*Artemisia tridentata*) and its associates are being encouraged as low-maintenance plants for highway plantings.

An ecological listing

The many uses for low-maintenance wildland shrubs plus the many different prevailing climatic conditions would make it extremely difficult to compile a single list of low-maintenance shrubs for a continent or other large diverse area. Several years ago, the Nevada State Highway Department needed information about shrubs and other plants that could be used for highway plantings and for erosion control. Because much of the State is arid, with hot summers and cold winters, survival under these harsh conditions was a prime requirement. Esthetic considerations were largely secondary. A 3-month study produced the University of Nevada College of Agriculture Bulletin B-7, "Review of Highway Planting Information Appropriate to Nevada" (Stark 1966). This bulletin included a review of highway planting practices of potential value in Nevada, and ecological listings for most of the shrubs and trees known to grow in the State.

Plan of the Nevada list

This paper describes the method used in preparing the *Review* and suggests improvements and extensions. The shrubs were grouped for three main types of plantings: (a) Intensive plantings for beautification where every needed condition could be provided; (b) intermediate plantings where care might be needed for a few months after planting or once or twice a year, and (c) nonintensive plantings for low maintenance, where little or no care was needed after planting. Uses for these three types included erosion control, noise reduction, screening from headlight glare, traffic guidance, safety, and control of snowdrifts.

Plants having special value for particular uses were noted within the three main lists. The intermediate and low-maintenance categories contained lists of "preferred plants"--those most likely to be successful--and "auxiliary plants"--those with potential value. All lists were further divided by major vegetation zones as described by Tueller (1969), such as the northern desert shrub, the salt-desert shrub, the southern desert shrub, the pinyon-juniper, and mountain brush.

Ecological characterization

The lists gave ecological characterizations for each shrub so that its known tolerance for various environmental conditions was included, as well as standard taxonomic and horticultural information. Thus the shrubs most nearly suited to the environmental conditions of any particular planting site could be selected and evaluated for actual maintenance requirements.

The ecological characterization for bitterbrush, sometimes called "antelope brush" (*Purshia tridentata* (Pursh) DC.) was published as shown on the following page.

Several hundred Nevada shrubs, both native and introduced, have been described in this Bulletin. This system has considerable value in screening native or introduced plants for maintenance requirements relative to different types of planting sites.

PURSHIA TRIDENTATA (Pursh) DC.
(Antelope Bush, Antelope Brush, or Bitterbrush)

ELEVATION--3,000 - 11,000 ft. (Munz)

VEGETATION--Sagebrush Scrub to Subalpine F.-e slope Sierra Nevada, B.C., Mont., New Mex. 3-N (Beatley 1965), ne. Nev. (Holmgren 1942), 8-0, 4-E, 13-WP, 2-L, 14-EL, 5-M (CNF) 15-H (Train 1939 H), Nevada (Munz 1959), 17-W, 9-S, 10-Ch, 11-La, 12-Ea.
Soils 20-60 inches deep, well-drained loams, sand (Summerfield, personal communication), dry slopes (Munz 1959) on clay pan (Moore 1937 H), soils at least 3 feet deep (Stanton 1959).

Soils--Alk.-acid or deep regosols, Brown Zone.
Sal.-alkali tolerant (Plummer 1960). Oregon (Driscoll 1962).

Moisture--12-25 inches precipitation (a), (Stanton 1959) arid flats, valleys, slopes of summits (McMinn 1951) 10-14 inches precipitation (S.C.S.)

INSECTS--none reported U.S.D.A. 1952
DISEASES--none reported U.S.D.A. 1953, 1960

COMMENTS--important browse species (Guilion 1964; McMinn 1951; Dayton 1931). Avoid use along roads in open range (N.S.) useful for erosion control (U.S.D.A. 1948), acid soil strains do poorly on limestone, some strains layer, somewhat fire resistant, sprouts freely (Plummer 1960, Stanton 1959). Bitter red juice within seed coat is rubbed on rocks and twigs by rodents leaving a coating resembling blood, rodents eat seeds, flowers may produce allergy in some persons.

AUTHORITY--Eamor A. Nord, or Augustus Hormay, U.S.F.S., PSW-Berkeley, Calif., Vines (1960), others.

LEAF CHAR.--Tomentose (white) below tridentate, small, 1-2 cm long (Munz 1959).

LEAF COLOR--dk. green above, white below (Munz 1959).

FLOWER COLOR--cream-yellow, small but conspicuous (Munz 1959), strong odor (N.S.)

FLOWER TIME--April-July (McMinn 1951), May-July (Munz 1959)

HEIGHT--1-3 m. (Munz 1959), also see Everett 1957 p. 178.

CULTURE--treat seeds with thio-urea, plant on bare, poor soil, added water improves survival (see U.S.D.A. 1948 on seeds).

PLANTING TIME--April-May (N.S.)

HARDINESS--Hardy in Nevada (N.S.)

EXPOSURE--n., ne slopes--Oregon e.-s.e. slopes (Driscoll 1962), sunny (vanDersal 1938).

SOURCE--seed collected easily in mid to late summer (Nord, p.c.).

NEVADA TRIALS--Dr. P. Tueller (Univ. of Nevada).

FRUIT--Achene, available in August (vanDersal 1938), bitter red juice.

BARK--Gray or brown ± glandular, young twigs tomentose (Munz 1959).

FORM--small to large much branched shrub (Munz 1959).

The first several items--elevation, vegetation, soils, moisture, exposure, insect pests, and diseases--give an environmental characterization that covers matters of concern in field planting of the listed species. Leaf color, leaf characteristics, flower color, flowering time, height, culture, fruit, planting time, bark, and form are important horticultural and field taxonomic characters. "Source" is useful because it tells where and when seeds or seedlings can be obtained. "Local trials" reports where the shrub has been planted experimentally. Detailed information on local trials could not be included in this brief statement. "Authority" lists some of the persons who have studied the shrub extensively; although incomplete, it provides a key to the literature. Special characteristics not appropriate to other categories are described in the "Comments" section.

These shrub descriptions would be improved by adding physiological characteristics because they would indicate why these shrubs can survive in one habitat but not in another. Additional data on physiology, life span, gene configuration, hybridization, growing season, wildlife value, hardiness, allergenic qualities, susceptibility to insects and diseases outside of their native habitat, and other physiological data should be added to show a more nearly complete characterization.

Environmental characterization

There are certain weaknesses in any direct application of an ecological characterization of a species as a guide to field planting. An introduced Rosaceae may fit one of the Great Basin environments quite well and to all appearances may be a successful introduction. But some native Rosaceae harbor a small bark beetle that is attracted to the introduced shrub, and the newcomer may lack resistance to the beetle. Whenever a low-maintenance shrub is moved from its native habitat (where it may have few natural enemies) to a similar habitat with different diseases, insects, and environmental stresses, there is no assurance that it will be "low-maintenance" in the new habitat.

Using the published ecological characterization to select satisfactory low-maintenance shrubs for a particular site requires measuring the extremes of the proposed planting site and matching these to the known tolerances of the potentially usable shrubs. When we have data on the soil moisture during the driest and wettest seasons, soil characteristics and chemistry, exposures, growing season, temperature extremes over a 20-year period, elevational limits, and other environmental conditions of the proposed planting site, it should be possible to select a usable shrub from the published list. If no serious disease, insect, or cultural problems develop, the final choice rests on the specific maintenance needs of the species chosen. Criteria must be set for low maintenance for any specific region and purpose. A weakness of this system is that too often we do not have adequate information about environmental extremes at projected planting sites, and usually neither time nor funds are available to get this information before decisions must be made. The literature does not contain sufficient information about tolerances of the shrubs. A further complication is our inability to measure environmental extremes in a useful way. Conventional measures of soil moisture are not applicable if the shrub being considered can utilize aerial moisture or moisture concentrated by distillation-condensation in the soil. Such questions arise as whether to measure soil moisture in the spring or at the period of greatest stress, or whether extremes of air or soil temperature have value without data on their duration.

An ecological characterization of shrub species, though necessary, is not by itself sufficient for the purpose of choosing low-maintenance shrubs. A detailed characterization of the habitats within the region is also needed. Soil maps are useful for areas that have extreme soil types, but if a shrub has strict requirements for temperature or moisture or other growth conditions, the soil map alone is inadequate. Maps showing precipitation or topography, or thermal patterns have similar limitations. What is needed is a systematic characterization of the range of conditions within a vegetation type or within divisions of a type.

A computerized system for selection of shrubs would be very useful. Data on the features of essentially homogeneous segments of many environments could be placed on punchcards as information became available. An obvious problem is to define meaningful environmental segments; but once a set of environmental characterizations had been determined, ecological characterizations for many shrubs could be matched against them by computer and finally sorted for specific low-maintenance requirements. Such a system could be of considerable value for introduced shrubs.

For example, let us consider a tall shrub (or small tree), growing to 13 m. called *Prosopis tamarugo* Phil., which grows in Chile. Studies by Sudzuki (1969) show that this shrub will grow even where there is a solid salt hardpan if a hole is broken through the hardpan. The shrub grows in areas that receive only 10-20 mm. precipitation every 7 years and have 10-15 days of fog per year. Sudzuki has also shown that the leaves can extract moisture from the air and suggests that even the roots obtain moisture from the air through the leaves and even secrete water into the soil. The plant requires watering for the first 6 months after planting and is then capable of surviving on its own, supposedly from aerial moisture (nocturnal relative humidity 40-100 percent). It is considered to be a good browse species for sheep although its fruit and leaves may not provide a complete diet.

The chances for success in planting *Prosopis* in the arid, warm deserts of Nevada could be calculated if complete ecological and environmental characterizations were available. Because this shrub appears to require high aerial moisture at night, there are probably few places where it could survive as a low-maintenance shrub in Nevada. Its temperature tolerances might limit its range. Such questions as the following would need answers: Does the shrub require salt-affected soils, or will it survive on any soil? Does it require high aerial humidity, or can it survive on ground water; if so, what quality of ground water? Would it pose possible insect or disease problems, or would it merely become a well-adapted weed in Nevada? These questions cannot be answered from our present knowledge of the plant and of our own desert environments.

A detailed ecological characterization of the shrubs of the world would be a major contribution to scientific knowledge. Even a limited listing such as the one quoted above, although far from complete, can be useful in screening potential introductions, locating shrubs that might meet special low-maintenance requirements for disease or insect resistance, or in providing a quick reference source for botanical research, range management, and other applications. An environmental characterization of shrublands throughout the world is a necessary part of this proposed system.

Soil cover and stabilization

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The use of shrubs for soil cover and stabilization automatically involves much more than this single purpose. Shrubs used to protect soil can also be of value as cover and as food sources for many kinds of wildlife. They may be used for landscape beautification, for the production of fruit to make jams and jellies, and for various other purposes. In fact, the species of shrubs intended for soil protection are usually selected because of these other values. These uses are being treated by others at this symposium.

The principal uses for shrubs have been:

1. As contour hedges on slopes to prevent washing, to provide wildlife with food and travel lanes, and to mark boundaries between different land uses. Generally, such hedges have been most commonly used in the eastern third of the country.

2. On the borders of woodlands for the protection of the interior from drying winds, for wildlife food and cover, and for soil protection, especially where cultivated areas are adjacent to the woodlands.

3. As borders on both sides of windbreaks or shelterbelts, both to help in prevention of soil blowing, and to provide additional food and cover for wildlife.

4. As protective plantings on sloped banks of streams, again with important secondary values for wildlife.

5. Plantings to help stabilize severely gullied areas set aside as wildlife areas. Usually the shrubs are best mixed with trees to give maximum interspersion and variety.

6. On road embankments and rights-of-way, with attention to landscape beautification. Some doubt has been expressed as to whether planting shrubs with fruits attractive to wildlife near highways is wise since the areas are of great danger for them.

7. On sandy areas, including sand dunes along the sea or lake coasts.

8. On spoilbanks along certain types of drainage ditches and from strip mines.

9. On lake or pond shores and their environs, both for landscape beautification and for wildlife food and cover. This would include plantings made above the impoundment to help slow down inflowing water which then drops whatever sediment load it may have been carrying.

In all such places, shrubs assist in protecting against soil movements by wind or water. It should be noted that few shrubs form a complete cover on the areas planted. Grasses and forbs must be used to supplement the shrubs, certainly when they are young, and sometimes even after the shrubs are older.

Most of the uses for shrubs that I have outlined are familiar to this audience. I would like next to outline an approach to the selection and use of species.

Plant growth regions

For the 48 contiguous States, Furman Loyd Mulford[1] identified 32 regions which he called plant growth regions. Growing conditions within each region are sufficiently similar so that if a plant will grow in one part of a region, it can be grown anywhere else in the same region. Mulford identified these regions empirically over many years of observation and trial. He also utilized data, especially for the Plains area, from crop successes and failures. Later, his regions were compared with soils and with Thornthwaite's climatic areas[2] and a few adjustments were made as a result.

What Mulford did, actually, was to use plants themselves as indicators. No thermometer, anemometer, rain gage, soil probe, or other instruments used individually or in combination are as accurate in determining an area in which a plant will succeed as is the living plant itself. Since Mulford's work, I have personally checked a large number of trees and shrubs grown in botanical gardens, experiment stations, arboretums, and hundreds of nurseries and home gardens. In addition, I have discussed the growth regions with Homer Shantz, Warren Thornthwaite, and a number of ecologists, soil scientists, and horticulturists. In summary, I have found very good agreement both on the concept and on the delineations on the map of the United States (fig. 1).

How this works may be illustrated by *Rhododendron catawbiense*, a shrub that is found in the southern Appalachians. It has been successfully grown for many years in Boston, and other parts of region 27; that is, it grows anywhere in the region. The same is true of *Leucothoe recurva*, *L. catesbaei*, the oakleaf hydrangea, several other rhododendrons or azaleas, *Fothergilla alnifolia*, a number of species of shrubby *Robinia* and many other shrubs, as well as trees. All these occur naturally either in the southern part of region 27 or in the central and southern part. All have been successful in the northern portion of the region.

On the Pacific Coast, Monterey cypress occurs just at the extreme southern end of growth region 1. In fact, the tree is found right on the boundary between regions 5 and 1. It has been successfully grown from south to north in region 1, and from north to south in region 5, thus being extended from a few locations to a coastal strip from Canada to Mexico.

Certain provisos must be made. For example, a shrub must be planted on a site comparable to the site where it succeeds. Thus a plant that grows in wet soil, or in full sun, or in half-shade, or on alkali soil, or in rich humus, should be planted on a similar site anywhere in the same plant growth region. Even this is not without

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[1]W. R. Van Dersal. Native woody plants of the United States. USDA Misc. Pub. 303. 1938 (see especially the article by Furman Loyd Mulford, p. 16-17.)

[2]Ibid.

U. S. DEPARTMENT OF AGRICULTURE

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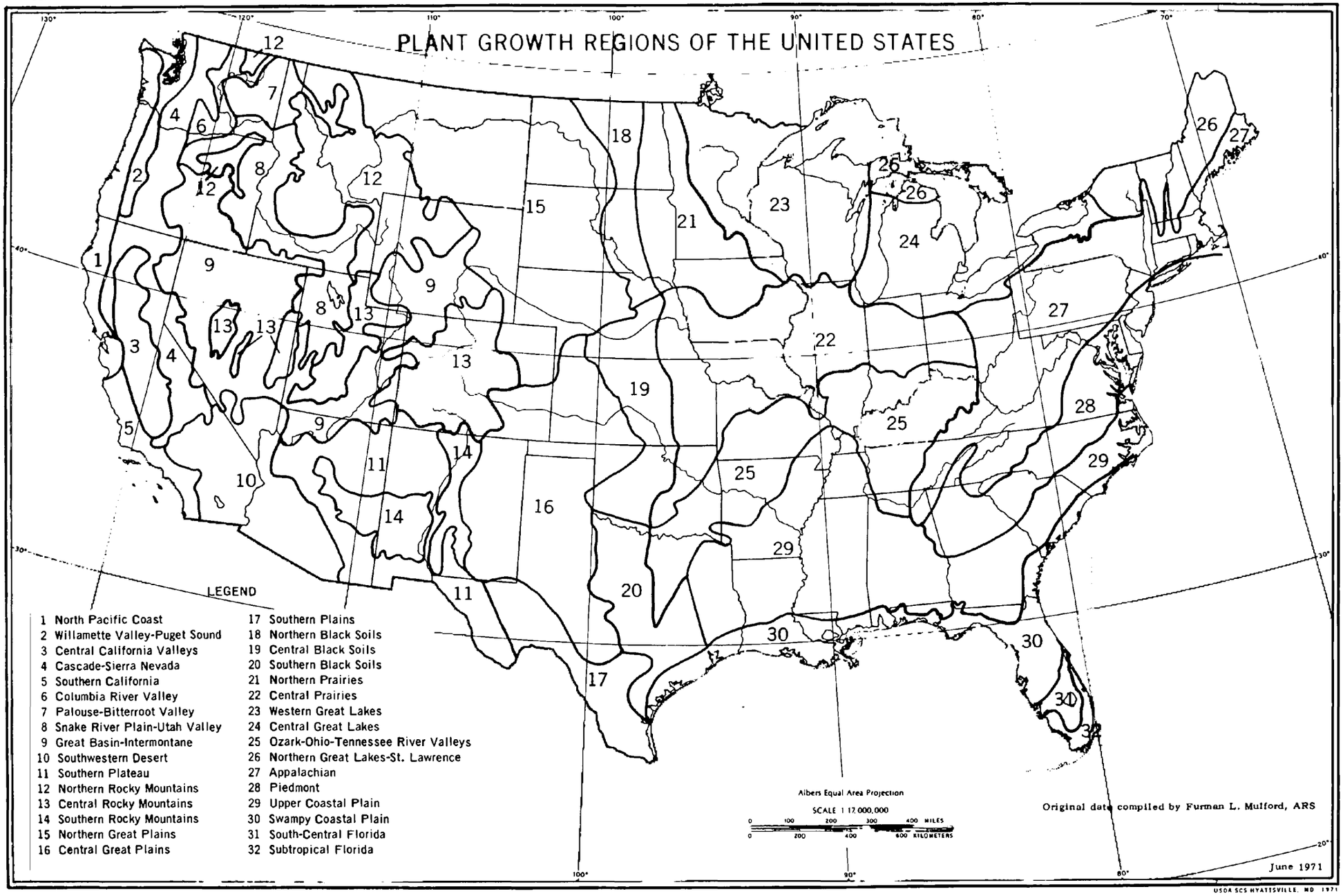

Figure 1

exception, e.g., the tamarack, *Larix americana*, and the bald cypress characteristically grow in swamps, but they will grow equally on well-drained soils.

A second proviso has to do with bacterial nodules. A shrub requiring this association (as in the case of alders, *Ceanothus*, *Elaeagnus*, *Shepherdia*, *Myrica*) cannot successfully be grown from seed unless the bacterium is present. This is a situation comparable to legume nodule formation without which, as in alfalfa, the plant grows poorly or not at all.

A third proviso is that occasional exceptions may be found. Such exceptions may be important since the exceptional plant may, in fact, be indicating that the growth region boundaries are not entirely accurate as drawn. It must indeed be said that the lines depicting the growth regions shoud not be thought of as absolute boundaries, but rather as generally separating one region from another. And lastly, local physiographic areas may change the picture somewhat, and thus it should be clear that the map shown is a generalized map showing only major areas.

With due acknowledgment that Mulford's rule and delineations are not necessarily precise and that there may be occasional exceptions to them, I believe the concept has great value. Using the growth regions, it is possible to extend the range of a native tree or shrub with far greater assurance than without them. Furthermore, the knowledge that a given native species *can* be used *throughout* any growth region in which it occurs, makes it possible to select useful shrubs or trees from a wider variety of species and thus enables greatly improved planning of projects.

Movements between regions

Nearly 100 years ago Charles Sprague Sargent found[3] that Douglas-fir grown from seeds obtained in the Rocky Mountains (growth regions 12, 13, 14) would succeed at Boston (27). Repeated trials with seeds from the Pacific coastal area (1, 2) and from the Cascade-Sierra Nevada Mountains (4) had failed at Boston (although successful in England at Kew). Later on[4] he reported the same thing to be true of *Abies concolor*, *Pinus ponderosa*, *Picea pungens*, *P. engelmannii* and *Thuja plicata*. Wilson in 1925 reported *Thuja plicata* to be doing well in the Arnold Arboretum,[5] as did Wyman in 1936.[6]

These and a goodly number of other species have by this time established the fact that trees from growth regions 1, 2, and 4 will fail in 27, but if the species occurs in 12, 13, or 14 either exclusively or in part, plants from these regions will succeed in 27. The reverse (i.e., 27 to 12, 13, or 14) is not true. Nor will trees from 27 succeed in 4, as shown in tests at the Wind River Arboretum in the Cascade Mountains of Oregon involving both conifers and hardwoods.[7]

A series of other relationships have been found. Some of these were published in 1938,[8] and others are being published in the 1972 Yearbook of the U.S. Department of Agriculture. Much of the work done has depended primarily upon trees, since there has been somewhat more interest shown in these larger woody plants.

A number of shrubs have also been tested that have displayed the same successes and failures as have the trees. These have included rather well-known cases of *Ribes*

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[3]C. S. Sargent. The Douglas fir. Garden and Forest 4:206 and 167. 1891.

[4]C. S. Sargent. Notes on cultivated conifers - VI. Garden and Forest 10:441-442. 1897.

[5]E. H. Wilson. America's greatest garden, p. 79, 80. 1925.

[6]Donald Wyman. A few evergreens. Arnold Arboretum Bull. Pop. Info. 4:93. 1936.

[7]T. T. Munger and E. L. Kolbe. The Wind River Arboretum from 1932-1937. 15 p. 1937.

[8]Van Dersal, op. cit.

sanguineum, *Holodiscus discolor*, and *Rubus nutkanus*, various species of *Arctostaphylos*, *Ceanothus*, and *Prunus ilicifolia* from regions 1 and 2 or 4 that failed repeatedly in 27. Shrubs ranging in the Rockies generally succeed, as for example *Mahonia aquifolium*, *M. nervosa*, *M. repens*, *Ribes aureum*, *Amorpha canescens*, and a number of others.

Results of movements between various plant growth regions that seem best established on the basis of sufficient accumulated data available to me are shown below. These movements are based entirely on trees and shrubs native to the United States.

1. Plants from regions 12, 13, and 14 are usually successful in 22, 24, 25, 27, and 28. The reverse is rarely true.

2. Plants from 27 and 28 are usually successful in 1, 2, 24, 25, and 29.

3. Plants from 1, 2, and 4 will usually grow in 28, 29, and 30, although success between 1, 2, and 28 appears to be a little less certain. Many attempts to grow plants from 1, 2, and 4, in 27 have failed.

4. Plants from region 5 usually succeed in 31 and 32, and the reverse also seems true.

5. Plants from region 20 usually do well in 29.

6. Plants from region 11 usually grow well in 5.

With the foregoing ideas in mind, I should like now to suggest that achieving success in moving shrubs from one part of the country to another could be augmented by employing the concept of plant associations, as used by the ecologists. Thus, if one or two species of a given association display success or failure in moving from one plant growth region to another, then it should follow that all associated species should succeed or fail similarly. A simple example, already referred to, would be that of the Pacific coastal form of Douglas-fir, commonly growing in areas with the red-flowering currant and ocean-spray. Douglas-fir from plant growth regions 1, 2, or 4 failed in 27 at Boston. On the basis of plant associations, it could have been predicted that the two shrubs associated with Douglas-fir would fail also--as indeed they did. I would suggest in this instance that other trees and shrubs found in the same association would also be likely to fail. Successful interregional transfers were made with the Rocky Mountain forms of Douglas-fir, ponderosa pine, and arborvitae, to region 27, for example, and shrubs associated with them should also succeed, as did Oregon grape, golden-flowering currant and others.

With respect to herbaceous annuals and perennials we are on much less certain ground. Such plants survive the winter either as seeds or underground parts. They are not subject to the year-round climatic factors that woody plants are, which must survive all of the seasons aboveground.

Transfers between countries

Although I do not know with certainty whether comparable plant growth regions have been delineated in other countries, I have found various climatic, physiographic, or soil provinces. One of these, as an example, is that of Oscar Drude for Germany[9] which divides the country into eight climatic zones. At any rate, various interchanges of woody plants between the United States and other countries of the world have been made. The results of at least some of the successful movements are fairly well-known to many nurserymen and horticulturists.

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[9]O. Drude. American forest trees in Germany. J. Forest. 23:646-647. 1900.

We have already noted that Sargent commented on the fact that Douglas-fir from the Pacific coastal area succeeded quite well in England although it failed at Boston (27). This interchange can be extended. Almost any woody plant native to 1, 2, or 4 has succeeded in England and southern Scotland. The same species generally succeed in New Zealand, certainly on the North Island, and the north half of the South Island.

Species native to growth region 5 have generally been successful in the States of Victoria and New South Wales in Australia, in the eastern, more humid crescent. Transfers from eastern Australia to growth region 5 have also been successful, especially with the eucalypts. It should be noted that a number of species of Eucalyptus require a mycorrhiza in order to grow successfully. Unfortunately for us, most of the best trees of this genus are in this category, and since we must import the plants as seeds, and cannot safely bring in soil without sterilizing it, we cannot get the trees.

A well-established interchange both back and forth has taken place between northern, central, and southeastern Europe and the Eastern United States, as pointed out many years ago by Wilson.[10] This same explorer pointed out that conifers from Siberia, northern China, and northern Japan had succeeded at Boston (27). Conifers fail at Boston from Mexico, Central America, southern China, Formosa, the Himalayas, southeastern Asia, and the entire southern hemisphere. At the same time, we may note that plants from the Himalayas, especially the rhododendrons, have done well in England, and thus, in all probability should do well in the Pacific area (1 and 2). Also, some woody plants from South America, such as *Escallonia*, have been successfully grown in region 5.

Summary

We may now summarize the foregoing data and concepts, as follows:

1. Plant growth regions delineated by Mulford can be used to determine with reasonable confidence that where a woody plant occurs in one part of a region it can be successfully grown in all parts of that region, provided it is planted in situations similar to those in which it grows as a native.

2. Certain transfers have proven possible between plant growth regions, and where these have been successful, it should be possible to make additional transfers of other species associated with the species tested.

3. It should be possible and practical to determine areas with a reasonable degree of precision in the rest of the world from which woody plants can be transferred to specific plant growth regions in this country and vice versa, with reasonable certainty of success.

Once the areas--both in other countries and in the United States--from which transfers have proven successful are known, then items 1 and 2 above may be applicable.

One additional point should undoubtedly be made. This is the fact that native shrubs, growing within range, are able to withstand competition under wild or semiwild conditions. Shrub plantings are not wisely made unless this factor is taken into consideration, notwithstanding occasional exceptions. But where the shrubs are introduced--either by extending the range of a native shrub within a plant growth region or by transfer from other growth regions, or from other parts of the world--some form of maintenance may be required and must be considered.

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[10] E. H. Wilson. *Aristocrats of the Garden*. New York. 1917.

Fire relations

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Like other kinds of plants, shrubs produce organic materials that will ignite and burn. Fires that destroy the shrub vegetation may be compared to a two-edged sword: they have both harmful and beneficial consequences. The harmful consequences of fire are well known. Brushland fires ranging out of control can trigger catastrophic destruction. The total acreage of brushlands burned in a year would run into the thousands.

Probably less well known are the beneficial effects of using fire as a land management tool under controlled conditions. Such a use of fire continues to be highly controversial. Nevertheless, studies have shown that fire stimulates production of browse, permitting deer populations to increase. Without further burning, shrubs become too crowded or trees close over to reduce productivity and quality of browse or forage. A fire can help prepare a site for planting by removing the cover, reduce undesirable competition, increase soil nutrients, and provide a firm seedbed with a soil surface favorable for covering seed (Bentley 1967).

Regardless of the position that the land manager takes in this controversy, we believe there is general agreement on this point: the protection of all vegetation from unwanted, damaging fires is essential to better wildland management.

A key to effective fire control and the successful use of fire in wildland management is the understanding of fire and its environment. Fire environment is the complex of fuel, topographic, and airmass factors that influences the inception, growth, and behavior of a fire (Countryman 1964). The fire environment can be represented by a triangle in which two sides coming to a point represent the fuel and topographic components and overlying them is the airmass component--the weather part of the fire environment. The current state of each component and its interactions with each of the other two and with the fire determine the characteristics and behavior of a fire at any given moment.

The topography and weather components are for all practical purposes beyond our control, but it is a different story with fuels. Man has a tremendous impact on wildland vegetation. Man can and does change the wildland vegetation as a fuel. And it is the fuel that provides the basic energy for fire behavior phenomena that we observe.

This paper describes the fuel component of shrubs and outlines their relation to fire environment.

Fuel loading

The fuel loading or the quantity of fuel available for burning is a property that is considered in almost every system of fuel classification. Fuel weight sets the maximum potential energy that may be released during burning. For a given rate of spread and constant heat yield, the fire intensity is directly proportional to the quantity of fuel that burns (Davis 1959).

The amount of shrub fuel--living or dead, in or on the ground or in the air--is found in almost infinite combinations of kind, size, and arrangement. The amount of fuel on a given acre varies from a few pounds where shrubs are small and sparse to 50 tons or more where shrubs are tall and dense (table 1).

Fuel loadings will vary according to the fuel type. Heavy chaparral dominated by California scrub oak (*Quercus dumosa*) and usually with lesser amounts of manzanita (*Arctostaphylos* spp.), mountain mahogany (*Cercocarpus* spp.), and other shrub species from 8 to 20 feet tall with stems up to 6 inches diameter contain from 30 to 50 tons of fuel per acre. Medium brush consisting of mixed chaparral typified by manzanita, ceanothus (*Ceanothus* spp.), chamise (*Adenostoma fasciculatum*), red shank (*A. sparsifolium*) and other shrub species ranging from 5 to 12 feet tall with stems up to 3 inches diameter contain between 15 to 30 tons per acre. Light brush stands, such as big sagebrush (*Artemisia tridentata*), coast sagebrush (*A. californica*), California buckwheat (*Eriogonum fasciculatum*), fourwing saltbush (*Atriplex canescens*), and other species that are usually less than 4 to 5 feet tall and stems less than 3 inches in diameter contain less than 15 tons per acre.

Observations have indicated that most fires do not consume living material larger than one-half inch in diameter. Thus, the proportion of smaller fuels is highly important in determining the character and behavior of a fire in shrub stands. The amount of fine fuel will vary between species and also between shrubs of the same species as well. Countryman and Philpot (1970) found that on the average, 61 percent of the fuel weight in chamise shrubs in southern California was in size classes one-half inch or less, but ranged from about 41 percent to more than 90 percent for individual shrubs. In northern California, the weight of material one-half inch in diameter or less for manzanita varied from 27 to 53 percent on four milacre plots analyzed. A similar range was found for manzanita and scrub oak in southern California (Firestop 1955).

Living fuels usually contain large amounts of moisture and hence do not burn well by themselves. But burning dead fuel can provide the heat necessary to dry the living fuel to a point where it will ignite and add to the total energy release from a fire. The amount of dead fuel, particularly in the small fuel size classes, can thus greatly affect its flammability. Differences in growth habits and effects of physiological stresses, such as drought and smog, cause wide variations in the amount of dead fuel between species and individual shrubs. In mature shrubs, Green (1970) found that dead fuel comprised about 35 percent of the total weight of standing mountain mahogany, 20 percent in chamise and manzanita, and 10 percent in scrub oak stands in southern California. Countryman and Philpot (1970) reported the amount of dead fuel ranged from 5 to 38 percent, with an overall average of 24 percent for 16 chamise shrubs analyzed from a typical mature stand. On the average, more than one-third of the total weight of the chamise fuel less than one-half inch in diameter was made up of dead fuel, but for some individual shrubs more than half the weight was dead material. The amount of dead fuel on the ground can also vary widely among species. Chamise produces little or no litter. On the other hand, in the northern California manzanita plots, ground litter amounted to 50 percent of the weight of the standing fuel.

The amount of fuel produced by brush stands is closely related to past fire history and to the type of vegetation that existed before burning. In chaparral and chamise stands, which in northern California are composed mostly of sprouting species, fuel

Table 1.--*Dry weight of fuel in brush stands in California*[1]

Brush cover type	Height	Aerial		Duff and litter	Total	Source of data
		Live	Dead			
	Ft.	*Tons/acre*				
		LIGHT BRUSH				
Big sagebrush-cheatgrass *(Artemisia tridentata-Bromus tectorum)*	< 4	[2]5.6	--	1.1	6.7	Frischknecht[3]
Coast sagebrush-deerweed *(A. californica-Lotus scoparius)*	4	3.7	2.8	6.7	13.2	Chandler (1955)
White sage-deerweed *(Salvia apiana)*	< 2	2.2	4.1	6.1	12.4	Chandler (1955)
Chamise-buckbrush *(Adenostoma fasciculatum-Ceanothus cuneatus)*	< 4	6.8	4.5	5.7	17.0	Chandler (1955)
Chamise (nearly pure)	5	7.2	5.9	3.3	16.3	Green (1971)
Chamise (unusually dense old stand)	--	--	--	--	14.0	Sampson (1944)
Coyote brush *(Baccharis pilularis)*	< 4	8.4	0.4	6.1	14.9	Chandler (1955)
		MEDIUM BRUSH				
Chamise-desert ceanothus *(Ceanothus greggii)*	6	23.5	6.0	--	[4]29.5	Green (1970)
Manzanita *(Arctostaphylos glauca & A. glandulosa)*	7	27.5	5.0	--	[4]32.5	Green (1970)
Manzanita	4	10.0	6.0	8.0	24.0	Carpenter and others (1970)
Mission manzanita-sumac *(Xylococcus bicolor-Rhus laurina)*	4-6	13.8	1.4	14.7	30.0	Chandler (1955)
Sumac	4-6	18.1	0.8	9.9	28.9	Chandler (1955)
		HEAVY BRUSH				
California scrub oak-toyon *(Quercus dumosa-Phontinia arbutifolia)*	> 7	15.1	5.2	6.0	26.3	Chandler (1955)
California scrub oak	> 6	20.1	3.2	21.7	45.0	Chandler (1955)
California scrub oak-buckbrush	> 6	30.9	3.4	5.6	39.9	Chandler (1955)
California scrub oak (nearly pure)	10	67.4	4.1	35.7	107.2	Green (1971)
Mountain mahogany *(Cercocarpus betuloides)*	11	29.0	19.0	--	[2]53.0	Green (1970)
Manzanita (nearly pure)	7	40.6	7.4	25.3	73.3	Green (1971)
Mixed chaparral	7	29.2	6.5	17.3	53.0	Green (1971)

[1]Data for big sagebrush-cheatgrass are stands in Utah.
[2]Includes live and dead aerial fuels.
[3]N. Frischknecht (1971) personal communication.
[4]Aerial fuel only.

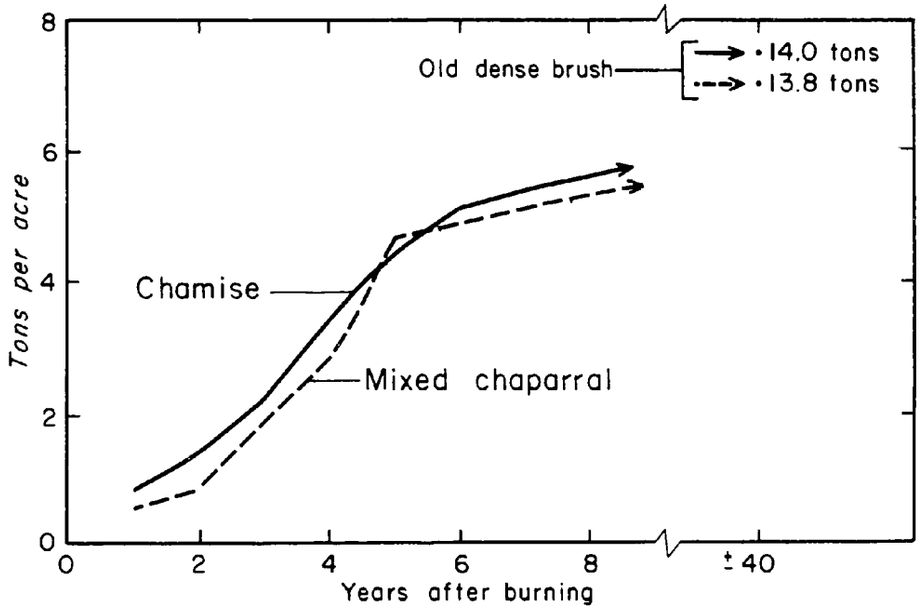


Figure 1.--The amount of aerial fuel produced by chamise and mixed chaparral vegetation in northern California accumulates and increases years after burning (adapted from Sampson 1944).

produced by shrubs built up rapidly after burns. Average annual increments ranged from 1,600 to 1,800 pounds per acre during the first 5 to 6 years, but thereafter the buildup accumulated at a lower rate (Sampson 1944) (fig. 1). Eventually, these brushlands accumulated about 14 tons aerial fuel by the time the stands were old, but plants remained dense and luxuriant.

Fuel arrangement

The arrangement of fuel is a more important measure of fire behavior than is fuel weight. In fact, fuel weight by itself may be a misleading measure of fire behavior (Chandler 1955). How the fuel is arranged within the stand along with other fuel elements, such as moisture content and chemical composition, has a greater influence on ignition time, rate of spread, burning time, and intensity of burns than the amount of fuel present.

Little is known about the physical characteristics of most shrub fuels. Countryman and Philpot (1970) recently developed techniques to determine the more important fuel characteristics of shrub plants. They measured volume, surface area, fuel particle density, and weights of plant components, and determined the range of values for chamise. From their data, they computed the fuel bed porosity and fuel loading (table 2).

A layer of pine needles 2 inches deep will give about the same fuel loading as does the material less than one-half inch in chamise--the fuel that produces most of the heat when shrubs burn. The surface-to-volume ratio of 1,741 for pine needles and 1,023 for chamise indicates that the size of the average fuel particle for the pine needles is much smaller than that of chamise. Yet, a burning pine needle bed will produce flames only 2 or 3 feet high, whereas flames from burning chamise stands can exceed 100 feet. The difference is probably due to the large dissimilarity in fuel bed porosity--1,024 for chamise and only 16 for the pine needles. The potential energy of the chamise fuel is released in a short time, while the more compact pine needle bed burns slowly.

Moisture content

The moisture content of wildland fuel has long been recognized as having a major influence on the ignition, development, and spread of fires. In fire-danger rating systems, fuel moisture is usually weighted heavily because it controls the current flammability of fuels--both living and dead (Davis 1959). When moisture content is high, fires are difficult to ignite, and burn poorly if at all. Moisture content of

Table 2.--*Fuel loading, surface-to-volume ratio, and fuel bed porosity of chamise, ponderosa pine litter, and cheatgrass fuels*

Fuels	Fuel loading	Surface-to-volume ratio	Fuel bed porosity[1]
	Tons/acre	*Sq.ft./cu.ft.*	*Cu.ft./cu.ft.*
		CHAMISE	
Entire plant	9.1	690	619
Foliage, stems	5.7	1,023	1,024
		PONDEROSA PINE	
Litter[2]	6.5	1,741	16
		CHEATGRASS	
Leaves[3]	.2	4,388	9,191

[1]Porosity: $\frac{\text{Fuel bed volume}}{\text{fuel volume}}$.
[2]2-inch depth. Source: Countryman (1969).
[3]Source: Brown (1970).

living fuels will range from about 35 percent to well over 200 percent, and in the absence of precipitation, from about 1.5 to 30 percent in dead fuels (Schroeder and Buck 1970).

Living and dead fuels have different water retention mechanisms and different responses to climatic conditions. The moisture content of dead fuel responds to relative humidity, temperature, and precipitation. The moisture content of dead twigs and small branches loosely arranged, such as those attached to plants like chamise, sagebrush, buckwheat, and many other species, responds quickly to changing weather conditions. In this characteristic, certain shrub fuels resemble grassland fuels, in which moisture content may be in approximate equilibrium with their immediate environment (Schroeder and Buck 1970). Since the dead fuel affects the way plants burn, fire behavior in shrub stands where a large proportion consists of fine dead materials can be expected to change quickly with variations in temperature and humidity (Countryman and Philpot 1970).

Moisture content of live plant materials depends largely on the shrub species--their physiological activity, growth stage, chemical composition--and on site conditions. The moisture content of the shrub components also varies widely--foliage and small twigs generally have a higher moisture content than the larger stems and boles. Peak moisture content occurs during the most active growth period, usually in spring when soil moisture is abundant and temperatures high enough for rapid plant growth. During this period the moisture content of the foliage may be 200 to 300 percent or more, and that of the stems will range upwards to 150 percent. The moisture content declines as the season progresses, rapidly at first, and then more slowly as plant growth matures and finally becomes dormant. During the dormant stage, the moisture content usually remains relatively constant.

Table 3.--*Moisture and ash content of shrub species, North Mountain Experimental Area, Riverside County, California, May 1971*

Species	Moisture content		Ash content
	Foliage and current leaders (1/8 in. dia.)	Foliage and stems (0.25 - 0.50 in. dia.)	Foliage and stems
	Percent		
Atriplex canescens	173	150	12.4
Atriplex polycarpa	347	228	12.2
Salvia sonomensis	277	213	9.8
Cistus ladiniferus	168	127	7.0
Cistus albidus x *C. crispus* - hybrid	205	152	5.7
Cistus villosus	201	143	5.7
Purshia glandulosa	154	131	4.6
Purshia tridentata	147	131	3.8
Adenostoma fasciculatum	[1]132	[1] 88	[2] 2.7

[1]Data adapted from Dell and Philpot (1965).
[2]Data adapted from Philpot (1970).

The moisture content of different shrub species can vary drastically on the same site at a given date; and possibly between varieties of the same species. In late May, the moisture content of eight introduced species being field tested for fire hazard reduction or other useful purposes in southern California ranged from 88 to 347 percent on the same site (table 3). A month later, three varieties of fourwing saltbush (*Atriplex canescens*) growing under identical conditions in the Pacific Southwest Station's Forest Fire Laboratory nursery at Riverside, California, had moisture contents ranging from 216 to 292 percent. During the 1965 fire season, chamise and fourwing saltbush growing under natural conditions on the same site were analyzed for moisture content throughout the season. The fourwing saltbush consistently had a much higher moisture content than the chamise (fig. 2).

The moisture content of living material possibly may increase as ash content increases. The eight introduced species were analyzed for their ash and moisture contents. Plants high in ash also had high moisture content (table 3). Linear regression yielded the equation:

$$M = 84 + 9.43\ A$$

in which

M = Moisture content in percent

A = Ash content in percent.

The variation in ash content accounted for about 60 percent of the moisture variation among these shrub species (fig. 3).

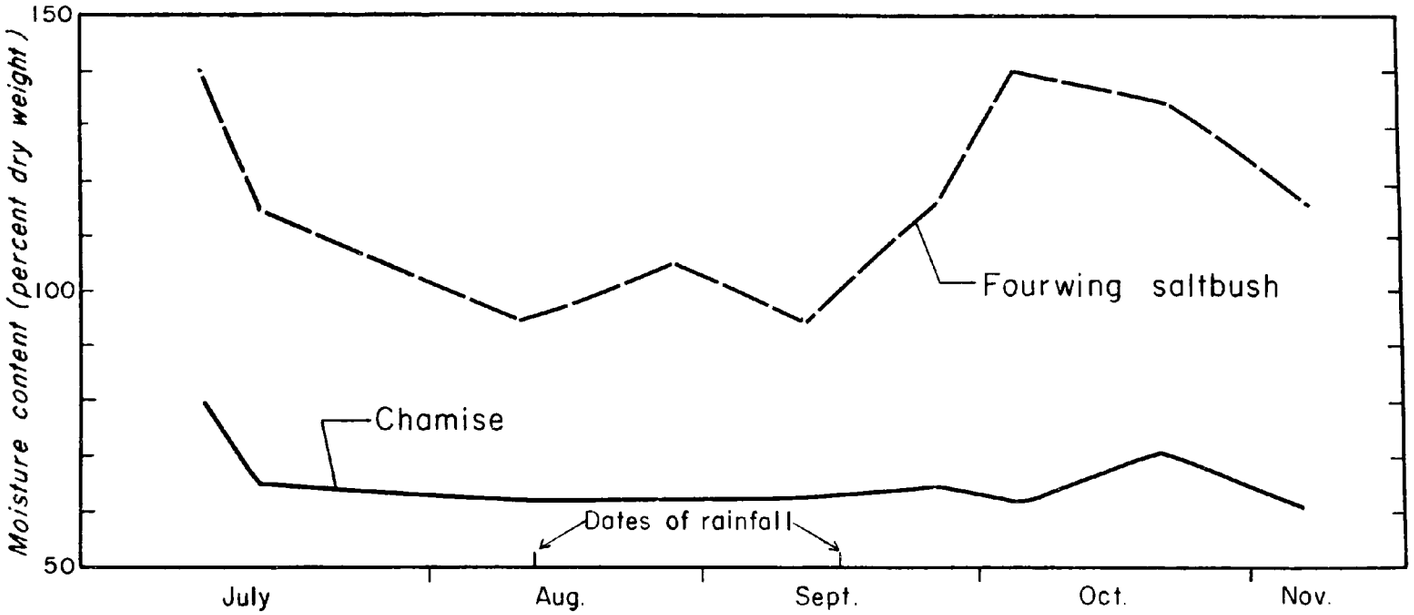


Figure 2.--The foliage moisture content of chamise and fourwing saltbush followed different patterns during the 1965 fire season. Plants were grown on similar sites near Moreno, Riverside County, California. Foliage included leaves and current stem leaders one-eighth inch or less in diameter.

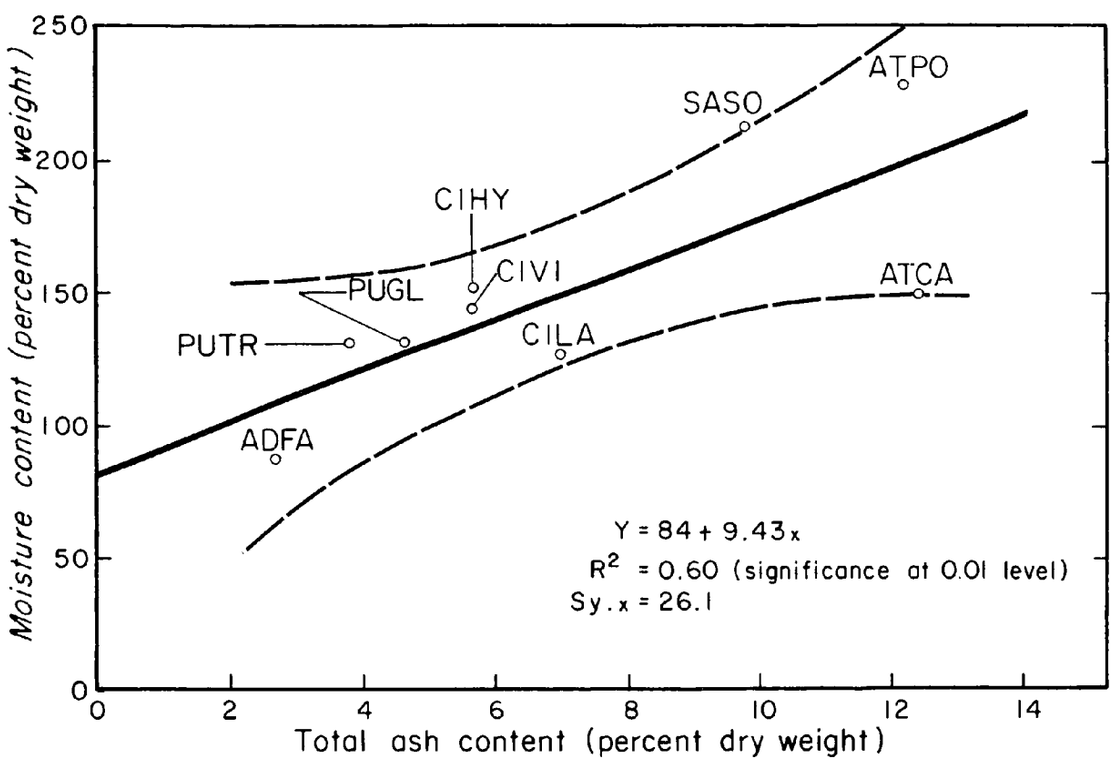


*Figure 3.--Plotted points relating moisture content to ash content for nine species represent mean values for foliage and stems less than one-half inch in diameter. Symbols used are: ATCA (*Atriplex canescens*), ATPO (*A. polycarpa*), SASO (*Salvia Sonomensis*), CILA (*Cistus ladiniferus*), CIHY (*C. albidus × C. crispus*), CIVI (*C. villosus*), PUGL (*Purshia glandulosa*), PUTR (*P. tridentata*), ADFA (*Adenostoma fasciculatum*). Data for ADFA adapted from Dell and Philpot (1965), Philpot (1970).*

We found a similar relationship between ash content and moisture content in three varieties of fourwing saltbush--two from California and one from Utah. The higher the ash content, the higher the moisture content in the foliage including current stem leaders, and in foliage and stems one-fourth to one-half inch in diameter. The analysis was done in early June 1971 in Riverside, California. If this same relationship holds for other species and other times, then the ash content could provide a gage to evaluate the ability of shrubs to obtain and retain moisture.

The generalization that moisture in live shrubs is usually closely related to soil moisture (Olsen 1960; Philpot 1963) does not always apply. Olsen reported that short-term weather fluctuations have an appreciable effect on green fuel moisture of shrub species, such as chamise. And Hanes (1965) found plant moisture increased as chamise growth resumed beginning in December even though soil moisture at 30 to 60 cm. depth remained below the wilting point until about 2 months later when first winter rains occurred. Presumably, atmospheric moisture plays some role in rehydration of shrub tissues for starting regrowth when plants are under moisture stress (Schroeder and Buck 1970).

Heat content and chemical composition

Most wildland fuels have heat values in the range of 7,500 to 10,000 B.t.u. per pound. Five species--*A. canescens*, *A. polycarpa*, *Cistus albidus* × *C. crispus*, *Purshia tridentata*, and *Salvia sonomensis*--we recently tested using standard bomb calorimetry methods (American Society for Testing Materials 1966) had heat values within this range. Two others tested--*A. cuneata* and *A. gardneri*--did not; they had values of 6,750 and 7,000 B.t.u. per pound, respectively. These heat values are considerably lower than have been reported for other shrub species (table 4). In some species, heat value is higher for the foliage than for the stems; for others the converse is true. It is likely that the variation in heat value is due primarily to differences in chemical composition (Countryman and Philpot 1970).

The effect of chemical composition of wildland fuel on fire characteristics has only recently received attention. The two most important classes of chemicals are (a) the high-energy ether extractives (waxes, oils, terpenes, and fats) and (b) the minerals which affect the pyrolysis of carbohydrates. Extractives appear to affect ignition time for plants. Mutch (1964) found that the ignition time for ponderosa pine powder and moss powder could be increased by removing the extractives. The pine had over four times more extractives than the moss. Philpot (1969) found that the burning rate of aspen leaves was reduced by solvent extraction. Philpot and Mutch (1968) found similar relationships for guava leaves treated with herbicides. Generally, ether extractives have a much higher heat value than other wood constituents. Thus, if they are present in sizable amounts, they can significantly affect the heat value of a fuel.

Work on pyrolysis of cellulose contaminated with inorganic compounds has led to the conclusion that the flammability of plant material is influenced by the presence of inorganic materials (Shafizadeh 1968). Broido and Nelson (1964) found that naturally dried and leached corn leaves were more flammable than unleached leaves because of differences in inorganic composition.

Philpot (1970) found that wildland fuels, such as shrubs, trees, and grasses, differing in mineral content showed quite dissimilar pyrolytic properties. Pyrolysis characteristics of plant materials with high ash content were similar to those of cellulose treated with flame-retarding compounds. In plant materials, such as produced by *Atriplex* and possibly other halophytes with high ash content, maximum volatilization rate and residue increased, and active pyrolysis began at a lower temperature than when ash content was low. Only some of the elements in plant ash actually affected pathways of pyrolysis. And noticeable effects that ash has on pyrolysis leveled off at 5 to 7

Table 4.--*Heat content of various shrub species*

Species	Foliage	Stems (1/4 - 1/2 in. dia.)	Source of data
	(B.t.u./lb.)		
Adenostoma fasciculatum	8,968	8,327	Countryman and Philpot (1970)
Arctostaphylos pungens	9,070	[1]	Davis (1968)
Arctostaphylos viscida	9,208	8,676	Countryman (1964)
Artemisia tridentata	8,527	[1]	Short and others (1966)
Atriplex canescens	8,475	8,280	[2]
Atriplex cuneata	6,750	[1]	[2]
Atriplex gardneri	7,000	[1]	[2]
Atriplex polycarpa	7,580	8,004	[2]
Cercocarpus montanus	8,483	[1]	Short and others (1966)
Cistus albidus x *C. crispus*	7,970	8,083	[2]
Purshia tridentata	8,760	8,773	[2]
Purshia tridentata - spring	8,703	[1]	Short and others (1966)
Salvia sonomensis	8,100	7,900	[2]

[1]Data not available.
[2]Data on file at Forest Fire Laboratory, Riverside, California.

percent of dry weight of fuel. Since all ash constituents are not equally effective, total ash content may not be a good indicator of the relative pyrolytic characteristics of natural fuel.

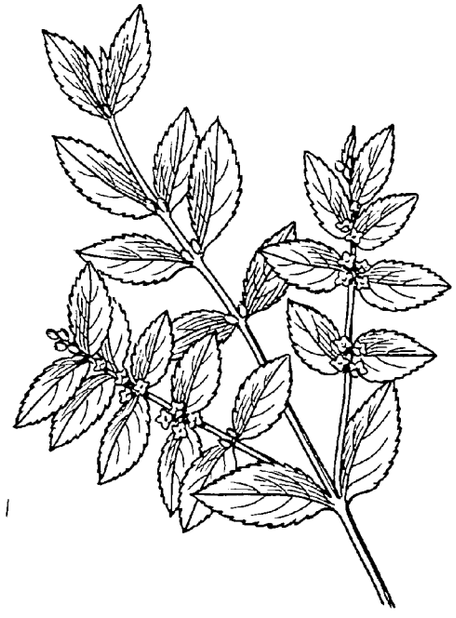
Although only certain chemical elements effectively inhibit pyrolysis, there is evidence that total ash content is closely related to moisture content of living material. This relationship suggests that the chemical constituents of shrubs that may have only a limited effect on pyrolysis could affect flammability through their effect on moisture content.

Slow burning plants

That some plants may be less flammable than others is the subject of research underway at the Station's Forest Fire Laboratory at Riverside, California. Such plants have been called "fire resistant." But the term "fire resistant" is misleading because almost all plants will burn if there is enough heat and other conditions are right (Green 1965; Maire and Goodin 1967). Instead of relying primarily on finding plants with fire retardant qualities in shrubs, we are now searching for shrubs of low growth habit and fuel volume that have a low heat output when they burn, that can be established readily, and that will grow under brushland site conditions.

The most promising low volume and low profile native shrubs that have been tested for southern California conditions are creeping sage (*Salvia sonomensis*) and certain *Atriplex*, such as Gardner's and Castlevalley saltbushes (*A. gardneri* and *A. cuneata*). Although fourwing saltbush (*A. canescens*) is not considered a low growing plant, it appears to be less flammable than most chaparral species. It can readily be established successfully by direct seeding and other means.

Creeping sage is a low plant that practically carpets the ground. It is native to California chaparral and once established, crowds out flashy fuel created by annual plants--mostly grasses. This plant can be started from either seeds, stem cuttings, or nursery stock, and plants have grown to a width of 4 feet and developed deep, extensive roots within 2 to 3 years in mountain test plots (Nord and others 1971a). Some saltbushes can be started also by direct seedings or transplants and grow rapidly on slightly acid as well as basic soils where they normally occur (Nord and others 1971b). Other low growing plants introduced from other countries may also be suitable, but need further testing before they can be recommended for extended use to reduce fire hazards in southern California. These introduced species include a hybrid rockrose (*C. albidus* × *C. crispus*) from the Mediterranean region, green galenia (*Galenia pubescens*) from South Africa, Caucasian artemisia (*Artemisia caucasica*) from the U.S.S.R., and saltbushes (*Atriplex* sp.) from Australia. Besides searching for and testing adaptability of low growing shrubs, we are working on methods for establishing and growing selected plants on wildland sites.



Medicinal values

Arnold Krochmal

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The majority of plants harvested for medicinal and pharmaceutical use in the world originate in wildlands. Generally people will harvest such plants and deliver them either dried or fresh to a collecting point from which they move into commerce for processing and resale in a packaged form or in a form modified to meet specific needs. The growing of medicinal plants as crops is a far smaller source of such materials. Examples of such programs would include the *Dioscorea* (yam), grown and harvested in Mexico and Guatemala, *Digitalis* (common foxglove), grown in Pennsylvania, and *Panax* (ginseng), grown in Kentucky (Krochmal 1968).

Dioscorea is the precursor source of cortisone and other steroid drugs. Although large quantities have been harvested in the wild, plantations also are producing high yields.

Foxglove, the source of *Digitalis*, the heart stimulant, is produced in row crops as well as in the wild.

Ginseng is grown to meet the excellent market in Hong Kong, Singapore, Malaysia, and other centers of Chinese population where it is used as a system tonic and sometimes as an aphrodisiac.

The development of an industry based on the harvest of wild indigenous plants for medicinal and pharmaceutical use depends on several interdependent socio-economic and ecological factors.

Ecologically, the most basic requirement is an adequate supply of the desired plants to make harvesting economically practical. There is no quantitative figure that will determine at what level of population density people can hope to make their labor input profitable. Experience of the harvesters will be the best determinant for this.

Economics

Deciding which plant or plants merit harvesting is a purely economic decision--which plants are marketable? I have been amused to hear people question the medical value of ginseng, *Panax quinquefolium*, which poses a moral question for doctors and philosophers to debate. In 1967, over $4,000,000 worth of ginseng left the Appalachian region (Krochmal 1968). That is justification enough for harvesting.

In some instances, technology may eliminate individual collecting of plant materials. Such an instance has come about in Appalachia. In past times, wild cherry bark was harvested by hand--now it is a byproduct of the lumber industry.

Conservation

Good management of such a program would urgently require some plans for regeneration if entire plants or roots are harvested although this would not be a problem in the case of shrubs harvested for leaves, flowers, fruits, and seeds. Regeneration would likely be adequate for future harvests. I think of our own perennial-rooted plant (*Trilisa odoratissima* (deer's tongue) (Krochmal 1969), harvested in Florida and Georgia for use as a tobacco flavoring, as an example of a plant that causes no problem in maintaining populations. Harvesting the leaves of this plant in amounts of over 3,000,000 pounds per year has not reduced populations because the roots are perennial, and regrowth is adequate. In other cases where *roots* are harvested, serious consideration must be given to repopulating the species. Again I think of our American ginseng source, *Panax quinquefolium*, whose roots are highly valued in areas of the world having large Chinese populations. This plant has been almost wiped out in Appalachia because of overharvesting. Fortunately some energetic growers in Appalachia and elsewhere have undertaken quite successfully to produce these plants as cultivars.

To guard future sources of such wild material and to protect plants from destruction, some program for educating harvesters in leaving a certain proportion of the wild plants intact is an urgent necessity. Where possible, studies of means of propagating threatened species may be justified. Our own work with *Lobelia inflata*, a wildland plant of Appalachia (Krochmal and others 1971; Krochmal and Wilken 1970), is an example of a planned attempt to protect a threatened plant from extinction by first studying how to get seeds to germinate. From our work we know how to propagate this plant and how to produce seeds and plants under cultivation.

Social aspects

Assuming that an adequate population is available, other factors more closely related to social forces must then be considered. Our own experience in Appalachia has shown that with a rising economy, people are less willing to harvest plants in the wild because the work is tiring and not of any particular prestige value in the community. I have noted not only in Appalachia, but in Greece, Honduras, Thailand, Afghanistan, the Virgin Islands, and other areas that prestige is not associated with *any* agricultural endeavor and that people prefer to work in urban areas or with machinery where recognition in the community is more readily available. This is a problem that must be solved by local methods of persuasion and motivation adapted to the culture of the peoples. For those living on cooperative farms, there are such possibilities as providing higher job credits for wild plant collecting than for the more desired jobs having higher recognition values. Blue-collar jobs in nearby urban centers such as Cincinnati have resulted in a population loss of one million people from Appalachia in 10 years and a decrease in pickers.

Collecting points

Collecting points are essential for the collector of wildland plants. These can be simply places where plants are brought when dried or can include drying facilities. The simplest facility would provide a dry surface, some source of shade, and ventilation. More complex facilities would include sources of artificial heat to provide more rapid drying for more valuable plants.

A collecting point can well be a building or complex used for packing fruits and vegetables at some other time of the year. In Florida, such a method is used for the harvesting, drying, and packing of *Trilisa odoratissima* (Krochmal 1969).

Movement of materials to processing plants or packaging plants is most economically effected in bulk shipments, particularly where an export market is sought. Too small a quantity of dried, semiprocessed or processed materials has no economic weight to make marketing sufficiently attractive economically. What quantity constitutes a proper

amount can be determined only through experience. Some form of private or government intervention to hold small quantities of materials until a marketable quantity is accumulated deserves consideration. Small collectors need their sales price when the material is sold. A reasonable return assures a continuing harvest.

Research

A sound and basic research program, using botanical and chemical approaches, can increase both harvests and cash returns. Although common knowledge is usually pretty sound in determining what parts of plants are required, chemical studies can help predict more accurately the optimum conditions for harvesting and, more specifically, what parts can be harvested. We have made such a study on *Lobelia inflata* (Krochmal and others 1970) to guide our harvesters in knowing the best time for collecting and have found, for example, that seeds in *Lobelia* add substantially to the total alkaloid harvest.

Another aspect of research is to determine new species for harvest. This is indeed a specialized field. I express the strongest disapproval of spectrum screening, in which without choice or selection, plants are examined for a wide range of organic substances such as alkaloids, resins, tannins, and so on. This sort of shotgun approach is expensive and time consuming; and the returns are not likely to cover the capital input for the investigation.

Two other roads are open for developing new plant resources. One is ethnobotanical, using folklore and village tales as a guide. Such a program is indeed valid. In India, a survey (Lelyveld 1967) is now underway to pinpoint references in the Kama-Sutra for plants used as abortifacients in legend. One promising plant has turned up. The use of *Rauwolfia serpentina* as a tranquilizing material for many, many generations was validated relatively recently although village tales have long before mentioned such a use.

It has been popular among westerners to deride the use of ginseng *(Panax quinquefolium)* as an aphrodisiac. Yet, recent research in Bulgaria (Petkov and Staneva-Stoicheva 1965), U.S.S.R. (Brekhman and Daroymov 1969), and Korea (Kim Chul and others 1970) have clearly demonstrated that roots of this plant have an identifiable clinical effect as systemic tonic and cortical stimulant.

Plants related to species of known value merit research. Two years ago while having lunch in New York with a friend associated with the United Nations Development Program, I mentioned my curiosity about *Phytolacca americana,* the common poke weed whose young leaves are harvested in Appalachia for canning as a green and whose berries are often fermented into wine or made into pie--although the roots are known to be highly toxic. My UN friend commented that in Ethiopia he had seen women use parts of the plant of the native *Phytolacca dodecandra* as a source of saponins for washing clothes in streams and that immediately above and below where they were washing, no snails could be found. The snail in the tropical world is an intermediate host for Bilharzia, a disease of man. On that basis we have undertaken a joint study with the University of Michigan of *P. americana* as a possible source of a naturally occurring molluscicide (Krochmal and LeQuesne 1970).

In our research we have taken a starting point of something known--a clue or indication--and have tried to follow that through. We have recently analyzed three native *Lobelias* for lobeline to see if they could be used as well as the one presently harvested (Krochmal and Chien 1971) and have found that one outyields the traditional lobeline source, *L. inflata.*

Summary

A viable and useful wildland medicinal plant industry requires available markets, a pool of labor, collecting points, marketing facilities, and a research program based on known information rather than long-range speculation and shotgun efforts. Conservation of species is essential for long-term yields.

Industrial raw materials from shrubs

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Plant materials of potential industrial value available from shrubs of arid regions are extremely varied. In this paper we are concerned with some of the chemical components that may have use in industry and medicine.

We know very little about the chemical composition of arid-land shrubs. The reasons can be summarized in one word: *economics*. Phytochemical research generally has been tied to the search for useful raw materials. It has been supported on the expectation of a favorable cost-return ratio. When the objectives of the search and the state of our knowledge dictate broad coverage, with many samples to be examined, as in our anticancer program, then species-rich vegetational areas are the best hunting grounds. Arid regions yield fewer samples per procurement dollar. When the objectives call for locating useful products in plants that can be developed as successful crops, then screening is concentrated on herbaceous plants, which are more suitable than shrubs for mechanized agriculture. So, much of the information on chemical composition of arid-land plants, shrubs in particular, has been produced more by accident than design. Nevertheless, shrubs of arid regions are a promising field for exploration for two reasons. First, we now have sufficient information about some categories of plant raw materials to permit a more intelligent search. Second, economic considerations that often work against arid-land shrub research are changing.

Any useful discussion of compositional attributes of shrubs of any region requires at least a partial inventory. Few such inventories exist. They must be compiled from floras and vegetation studies. Where habit information is lacking, it is difficult to check on whether all shrubs and only shrubs have been included. Not all arid regions are adequately covered by published floras or vegetation studies.

The literature on poisonous and medicinal plants is both extensive and impressive. Comprehensive monographs are available on various categories of raw materials from plants--the essential oils (Guenther 1948-1952), waxes (Warth 1956), alkaloids (Raffauf 1970; Willaman and Li 1970), fats (Eckey 1954; Hilditch and Williams 1964), gums (Howes 1949; Mantell 1947; Smith and Montgomery 1959) and others. Also, a vast literature has accumulated dealing with the systematic distribution of particular chemical constituents in plant groups (Alston and Turner 1963; Swain (ed.) 1963, 1966). Then there are the well-known dictionaries of economic plants--local, regional, and worldwide--that provide concise summaries of compositional and use data for numerous species of plants. Finally, numerous articles in journals of economic botany, phytochemistry, and pharmacology deal with plant raw materials and their uses. All these sources provide information about arid-land shrubs. This review is based on as complete a list as possible of the shrubs of all regions for which we have any data on shrub composition. Unfortunately, not all of the world's arid regions are represented.

A specially noteworthy source of information on compositional characteristics of arid-land shrubs is the voluminous and still growing screening data collection of the New Crops Research Branch of the USDA Agricultural Research Service. These data have been generated by large, objective screening programs during the last 20 years undertaken with chemists of the USDA Utilization Research and Development Divisions (now Marketing and Nutrition Research Divisions), the National Cancer Institute, the National Institute of Arthritic and Metabolic Diseases, and the National Heart Institute, all of the National Institutes of Health, and various State and private laboratories. Some 40,000 plant samples, representing nearly 20,000 plant species, have been evaluated as sources of seed oils, proteins, gums, fiber for paper pulp, anticancer agents, steroidal-sapogenins for corticoid drugs, alkaloids useful in controlling cardiovascular irregularities, and many other compounds having potential use.

Some data have been published and more are being prepared for publication (Correll and others 1955; Earle and Jones 1962; Jones and Earle 1966; Jones and Wolff 1960; Nelson and others 1966; Perdue and Hartwell 1969; Tookey and others 1962; Tookey and Jones 1965; VanEtten and others 1967; Wall and others 1954, 1961).

Both published and otherwise available information has been used in this attempt to characterize shrubs and groups of shrubs according to their potentially useful chemical components.

Seed components

Data on seed composition are available for 346 arid-land shrub species distributed in 231 genera and 72 families. On a family basis, this is rather broad sampling, but the list we compiled of the world's arid-land shrubs (perhaps 25-30 percent of the total number) includes some 3,000 species in 800 genera of 124 families. Time and space limitations do not permit complete reporting of these analytical data in this paper.

Seed oil and protein

New seed oils may provide valuable chemical raw materials for industry, with high-protein meal for food or feed as an important coproduct of oil extraction. The list of selected shrub species known to have high content of oil, protein, or both (table 1) confirms belief that shrubs are promising sources of raw materials. Both *Simmondsia chinensis* (jojoba) and *Dimorphotheca cuneata* (capemarigold) produce seed oils of known high potential.

Chemists and botanists of the Agricultural Research Service intensively studied members of *Dimorphotheca* and related genera of the tribe Calenduleae (family compositae) in their search for new industrial oilseed crops (Barclay and Earle 1965; Earle, Wolff, and Jones 1960; Earle and others 1962; Earle and others 1964; Jones and Wolff 1960; Smith and others 1960). Their survey pursued promising leads discovered in the ARS seed-screening program. Data on comparative phytochemistry and taxonomic relations are highly valuable in the search for potentially valuable plant constituents.

Members of the Calenduleae range in habit from diminutive annuals to arborescent shrubs. Fruit types vary from membranous-winged achenes to bony-hulled, nutlike structures to drupes. As interpreted by Norlindh (1943, 1946), the monographer of the group, this tribe consists of nine genera, eight of which are restricted to the Old World. There the tribe has two main centers of distribution: the Mediterranean region and southern Africa. In southern Africa the tribe has attained its greatest differentiation into genera and species and is represented by *Dimorphotheca* (seven species), *Castalis* (three species), *Osteospermum* (67 species), *Chrysanthemoides* (two species), *Gibbaria* (two species) (Norlindh 1943), and *Garuleum* (eight species) (Willis 1966). Only *Calendula* (20-30 species) (Willis 1966) and *Dipterocome* (one species) occur in the Mediterranean center. The sole representative of the tribe in the New World is *Eriachaenium magellanicum* of Tierra del Fuego.

Table 1.--*Seed oil and protein content of selected arid-land shrubs*

Shrub source	Data on component analyzed			Shrub source	Data on component analyzed			Shrub source	Data on component analyzed		
	Wt./1,000 g.	Protein %	Oil %		Wt./1,000 g.	Protein %	Oil %		Wt./1,000 g.	Protein %	Oil %
SANTALACEAE				*Prosopis juliflora*	32.0	39.9	6.6	*Argania spinosa*	237.0	19.4	60.4
Osyris alba	105.3	10.6	36.1	*Willardia mexicana*	81.1	32.9	25.8	STYRACACEAE			
CHENOPODIACEAE				ZYGOPHYLLACEAE				*Styrax officinalis*	56.6	16.5	50.8
Eurotia lanata	3.0	34.7	17.7	*Balanites aegyptiaca*	890.0	21.9	45.7	OLEACEAE			
Salsola vermiculata	1.4	47.4	15.2	*Larrea divaricata*	2.4	29.0	12.9	*Menodora scabra*	2.0	25.7	32.0
Suaeda fruticosa	0.1	19.8	20.7	MALPIGHIACEAE				LABIATAE			
CAPPARACEAE				*Mascagnia macroptera*	26.0	33.7	33.2	*Hyssopus officinalis*	1.0	27.0	29.4
Capparis ovata	10.0	23.7	30.9	EUPHORBIACEAE				*Lavandual multifida*	0.4	20.7	25.7
Isomeris arborea	44.0	40.6	42.0	*Euphorbia squamigera*	7.5	24.1	34.2	BIGNONIACEAE			
ROSACEAE				BUXACEAE				*Chilopsis linearis*	7.2	35.1	32.7
Fallugia paradoxe	1.6	30.6	36.8	*Buxus sempervirens*	13.8	21.8	44.3	*Rhigozum trichotomum*	21.8	26.8	20.1
Prunus institia	85.2	28.4	50.0	*Simmondsia chinensis*	835.0	14.8	53.5	GOODENIACEAE			
LEGUMINOSAE				CELASTRACEAE				*Scaveola plumieri*	60.6	19.2	66.7
Acacia constricta	18.4	41.9	11.0	*Euonymus verrucosus*	33.0	19.2	52.5	COMPOSITAE			
Brongniartia alamosana	10.0	26.9	33.9	STAPHYLEACEAE				*Baccharis sarthroides*	0.4	23.8	31.3
Calliandra eriophylla	23.1	38.9	16.4	*Staphylea pinnata*	90.0	33.6	42.7	*Chrysanthemoides monilifera*	10.4	--	49.0
Cassia biflora	10.0	23.1	4.4	RHAMNACEAE				*Chrysothamnus parryi*	2.7	32.2	28.0
Ceratonia siliqua	200.0	17.5	1.5	*Paliurus spina-christi*	17.0	32.5	21.0	*Dimorphoteca cuneata*	3.3	38.2	32.2
Coursetia glandulosa	15.8	55.6	17.1	*Rhamnus cathartica*	13.1	20.5	24.6	*Euryops athanasiae*	3.8	22.8	40.4
Genista tinctoria	4.2	44.3	6.2	*Ziziphus obtusifolia*	16.6	21.5	28.8	*Flourensia pringlei*	26.0	46.2	30.6
Lysiloma divaricata	30.3	33.1	12.9	THYMELAEACEAE				*Gutierrezia sarothrae*	0.2	32.3	31.8
Mimosa palmeri	7.4	36.9	6.1	*Daphne gnidioides*	12.8	30.7	58.1	*Osteospermum sinuatum*	3.7-	41.9	42.6
Parkinsonia aculeata	170.0	21.2	3.8	SAPOTACEAE				*Parthenium argentatum*	0.4	34.9	24.0

Seed oils from 88 samples, representing 29 species in five genera, were analyzed in our survey of the Calenduleae (Barclay and Earle 1965; Earle and others 1964). All of the oils contained as a major constituent either conjugated dienoic (dimorphecolic) acid or conjugated trienoic acid. Dimorphecolic acid (9-hydroxy-*trans*-10, *trans*-12-octadecadienoic acid) has unique structure and a high chemical reactivity; it offers many possibilities for modification to meet a variety of industrial requirements. Possible applications for the glyceride oil itself, dimorphecolic acid, or derivatives of the acid include protective coatings, urethane foams, and chemical adducts as synthetic intermediates or components of plastics and resins. The conjugated trienoic acid, though of less interest, makes up the major portion of most of the analyzed Calenduleae seed oils. These triene-rich oils may have potential as quick-drying vehicles for paints, lacquers, and varnishes (Trotter, Poats, and Wolff 1962). However, these uses require that the oils become commercially available at competitive prices.

The lower portion of figure 1 illustrates the range of dienoic and trienoic acids in genera of the Calenduleae surveyed. Dimorphecolic (dienoic) acid is the characteristic component in all analyzed samples of *Dimorphotheca* (five species) and *Castalis* (one species). It is also the principal acid of five species of *Osteospermum* belonging to section *Blaxium*. In 11 of the 15 sections of *Osteospermum*, one or more species have been analyzed, and only those belonging to section *Blaxium* contain high percentages of dimorphecolic acid. All other analyzed species of the tribe contain relatively high percentages of conjugated triene and little or no dimorphecolic acid (14 species in 10 sections of *Osteospermum*, two species of *Calendula*, and two of *Chrysanthemoides*).

This review indicates that distribution of the two major fatty acids in genera of the Calenduleae is not random. In our seed-screening experience, correlations between plant chemistry and morphology are frequent. The concepts of interrelationships and phylogeny in the Calenduleae presented by Norlindh (1946) are based primarily on morphological criteria. A broad summary of Norlindh's views of evolution in the tribe is depicted in the upper portion of figure 1. Theoretically the tribe Calenduleae first crystallized out as a primitive *Dimorphotheca* and, to begin with, comprised only species that produced both ray and disk achenes. From the ancestral Dimorphothecas, two main lines developed by subsequent reductions of the pistils in either the disk or ray flowers. Extant members of *Dimorphotheca* are considered primitive because female-fertility is retained in both the disk and ray flowers. The small genus *Castalis* differentiated from *Dimorphotheca* through reductions of the pistils of the ray flowers and is the only representative of this line of evolution. The remaining genera (*Osteospermum*, *Chrysanthemoides*, *Gibbaria*, and *Calendula*) evolved through reductions of the disk pistils and represent the dominant evolutionary trend in the Calenduleae.

Working from studies of style and achene morphology, Norlindh has emphasized in particular the close relationship of *Castalis* and section *Blaxium* of *Osteospermum* to *Dimorphotheca*. Judging from the style types, Norlindh hypothesized that some species of *Castalis* and section *Blaxium* have differentiated from *Dimorphotheca* comparatively recently. Occurrence of high percentages of dimorphecolic acid in the seed oils of *Dimorphotheca*, section *Blaxium* of *Osteospermum*, and *Castalis* substantiates his views that these taxa are closely related and lends credibility to his phylogenetic concepts. It is also solid evidence that even limited sampling can provide reasonably reliable leads that should be useful in focusing a search for a given chemical constituent of plants.

Seed gums

The only domestic sources of plant gums are seaweed products and guar (*Cyamopsis tetragonoloba*). Guar has become established in the southwestern United States as a minor crop; domestic production supplies only a small fraction of total consumption in the United States. Gums are widely used in industry as sizing, thickening, or stabilizing agents. This market is expanding and there appears to be good opportunity for a domestic crop source of glactomannan-type seed gums.

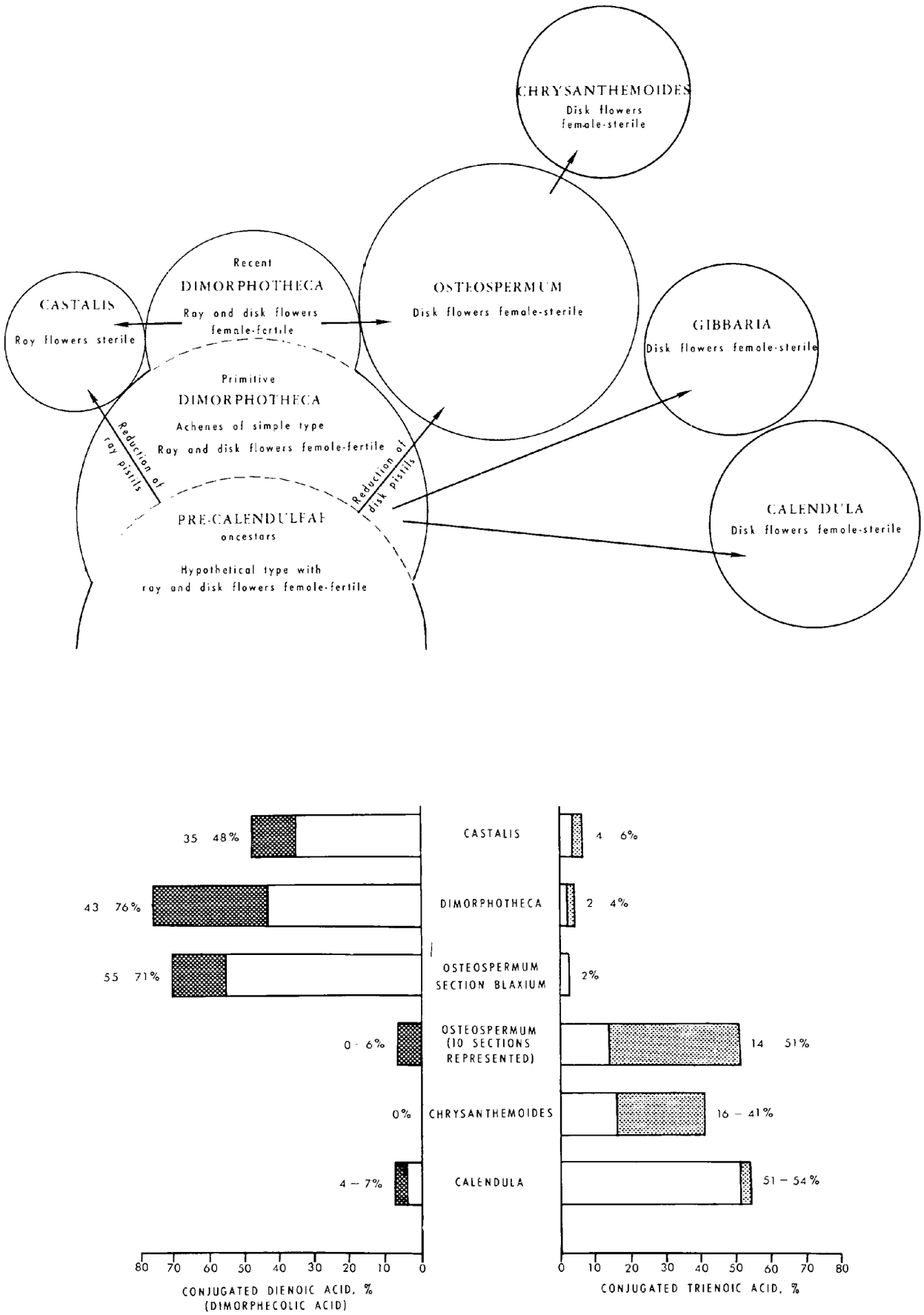

Figure 1.--Top: *Phylogenetic chart of the Calenduleae. (Adapted from Tycho Norlindh, 1946).* Bottom: *Range of conjugated fatty acids in taxa of the Calenduleae.*

Table 2.--*Seed gum content of arid-land shrubs of leguminosae*[1]

Shrub source	Gum, percent of air-dry seed		Weight of seed
	N-free	Crude	(g./1,000)
SUBFAMILY MIMOSOIDEAE			
Lysiloma divaricata	--	6.1	30.1
Mimosa palmeri	14.2	--	7.4
Prosopis juliflora	14.7	--	32.0
SUBFAMILY CAESALPINIOIDEAE			
Cassia armata	10.0	--	28.0
C. biflora	25.0	--	10.0
Ceratonia siliqua	20.1	--	200.0
Parkinsonia aculeata	28.1	--	170.0
SUBFAMILY PAPILIONOIDEAE			
Amorpha canescens	2.8	3.0	--
Cytisus scoparius	8.9	--	10.6
Dalea nutans	--	6.9	3.4

[1]Compiled from Tookey and Jones (1965).

Seed gums are distributed rather widely among the flowering plants. In the ARS seed-screening program, 300 species in 139 genera of 31 families were tested for the presence of water-soluble or water-swelling polysaccharide gum (Tookey and others 1962; Tookey and Jones 1965). Only seven of the 31 families had at least one representative with 10 percent or more gum in its seed. Of these seven families, Leguminosae appears to be by far the best source of seed gum. Among the three subfamilies of the Leguminosae, the Caesalpinioideae stand out as potential gum sources. This is true within the category of arid-land shrubs (table 2).

Jojoba—an illustration of changing economics

The fact that the economics of shrub utilization may change is illustrated by the desert shrub jojoba (*Simmondsia chinensis*). Half of the bean-sized seed of jojoba (endemic to the Sonoran Desert) is composed of a liquid wax made up of esters of long-chain (C_{20} and C_{22}) fatty acids and alcohols rather than esters of glycerine. The expressed and unrefined liquid wax has frequently been proposed as a substitute for winterized sperm whale oil (Daughtery, Sineath, and Wastler 1958).

American industry annually uses approximately 50 million pounds of winterized sperm oil, principally in the manufacture of special lubricants. A substantial portion of this sperm oil is required for applications for which there are now no known replacements. Certain materials are expected to be suitable on the basis of composition and properties; of these, jojoba is a prime example. A patent (Wells 1948) describes the sulfurization of jojoba oil to give properties similar to, and in some respects even better than, those of sulfurized sperm oil (table 3). However, before a product can properly be called a sperm oil substitute, actual performance in the application in question must be demonstrated.

Formerly, sperm whales were exploited for their oil and jojoba was in a poor competitive position. Because protection of these rare whales may soon bring restrictions on their use for oil, the economic balance *may* be shifting in favor of jojoba. Other seed oils from plants having apparently greater crop potential than jojoba are

Table 3.--*Properties of sulfurized oils*[1]

Characteristic	Jojoba	Sperm
Gravity, ° API	23.5	23.5
SSU vis./100° F.	151	155
Pour Point, ° F.	-20	-25
Flash Point, ° F.	340	340
Fire Point, ° F.	385	385
Sulfur Content, %	3.58	2.79

[1]From Wells (1948).

likely to be its most serious competitors. This large, long-lived shrub requires at least 5 years to come into seed production (Gentry 1958). Jojoba has been cultivated on a very small scale but essentially no research has been done on its cultural requirements and the possibilities for mechanical harvest of its nuts.

Alkaloids

Plant alkaloids, because of their marked physiological activity in animals and their actual or potential medicinal value, have invited considerable phytochemical and pharmacological research. According to Willaman and Li (1970), "The amount of data on alkaloid plants published in the last ten years exceeds that of all records accumulated in the past up to 1957. This period of active research in this area not only witnesses intensive studies on certain particular species or genera, but also extensive surveys of nearly all groups of plants in many parts of the world." Our limited survey of arid-land shrubs revealed 202 alkaloid-bearing species distributed among 129 genera and 49 families. The families we found to be richest in alkaloid-containing species are listed in table 4.

Several species, notably *Anabasis aphylla* (Chenopodiaceae) of Russia and the *Duboisia* spp. (Solanaceae) of Australia, have been exploited as alkaloid sources. Undoubtedly many alkaloid-bearing shrubs await discovery and some of these may prove to have commercial possibilities. Our investigation revealed that only 16 percent of the 800 genera encompassed in our survey included alkaloid-bearing arid-land shrubs. Although 43 percent of the genera surveyed are known to include some alkaloid-bearing species, these are not necessarily shrubby or arid-land plants. Such figures suggest that the arid-land shrubs have been inadequately sampled for alkaloids.

Anticancer agents

Repeatedly, the search for plant compounds having unusual chemical structure or unique biological activity has been rewarded. So it is in our search for plant sources of anitcancer drugs. In the 12 years since the National Cancer Institute and the Agricultural Research Service joined forces in a program to screen plant extracts for anticancer activity, crude extracts of some 1,300 plant species have been shown to inhibit cancer growth in laboratory animals. Purified active agents from a number of these are now being evaluated in the clinic, others have been approved for clinical evaluation, and still more are undergoing preclinical pharmacological testing. Chemists are working at isolation and purification of active agents from many other plant extracts. To protect their interests in rights of discovery and publication, we are not at liberty to name the plant sources of these confirmed active extracts. Those that have moved into clinical and preclinical phases of the evaluation program have been identified in part by Perdue and Hartwell (1969). Many species whose extracts show anticancer activity are in families that include arid-land shrubs. Distribution of these species, some of them arid-land shrubs, is shown in table 5.

Table 4.--*Families rich in alkaloid-bearing arid-land shrubs*

Family	Alkaloid-bearing shrubs	
	Species	Genera
Ephedraceae	12	1
Chenopodiaceae	25	11
Leguminosae	46	23
Euphorbiaceae	6	5
Rhamnaceae	6	4
Apocynaceae	6	5
Labiatae	4	4
Solanaceae	9	6
Compositae	22	14

Table 5.--*Incidence of plant extracts showing anticancer activity in families containing arid-land shrubs*

Family	No. of species/genera		Family	No. of species/genera		Family	No. of species/genera	
Pinaceae	26	5	Rutaceae	16	13	Rhizophoraceae	3	3
Cupressaceae	35	10	Simaroubaceae	7	6	Combretaceae	7	4
Ephedraceae	3	1	Burseraceae	10	1	Myrtaceae	25	11
Agavaceae	35	5	Meliaceae	13	8	Onagraceae	13	5
Casuarinaceae	2	1	Polygalaceae	3	1	Araliaceae	7	5
Salicaceae	4	2	Euphorbiaceae	43	20	Ericaceae	19	12
Juglandaceae	3	3	Buxaceae	1	1	Myrsinaceae	9	6
Fagaceae	14	4	Coriariaceae	1	1	Plumbaginaceae	2	2
Ulmaceae	8	5	Anacardiaceae	16	11	Ebenaceae	2	2
Moraceae	16	8	Celastraceae	14	7	Oleaceae	6	4
Proteaceae	2	2	Aceraceae	5	1	Apocynaceae	43	21
Aristolochiaceae	5	2	Sapindaceae	10	8	Asclepiadaceae	26	14
Polygonaceae	25	9	Rhamnaceae	6	4	Convolvulaceae	9	4
Chenopodiaceae	3	3	Vitaceae	5	4	Polemoniaceae	7	4
Nyctaginaceae	7	6	Tiliaceae	4	4	Boraginaceae	12	8
Berberidaceae	7	4	Malvaceae	7	1	Verbenaceae	8	4
Minspermaceae	8	5	Sterculiaceae	5	4	Labiatae	12	10
Capparaceae	2	2	Guttiferae	7	4	Solanaceae	14	8
Crassulaceae	12	9	Tamaricaceae	1	1	Scrophulariaceae	14	9
Saxifragaceae	8	6	Cistaceae	2	2	Bignoniaceae	5	5
Rosaceae	40	23	Cactaceae	6	5	Rubiaceae	32	23
Leguminosae	119	69	Thymelaeaceae	7	4	Caprifoliaceae	8	2
Zygophyllaceae	2	2	Elaeagnaceae	3	3	Compositae	120	73

The classes of chemical compounds in these active agents are varied. Alkaloids, saponins, tannins, phytosterols, lignins, and proteins are some of the more familiar classes. The large number of desert shrubs known to contain alkaloids, plus the many more that can be presumed to contain them, seem to offer promising possibilities of search for anticancer activity, as would the many shrub groups known to contain saponins.

Conclusions

Our extensive survey confirms the conclusion reached by Robert R. Cruse (1949) that "although chemical utilization of desert plants is not immediately feasible, except perhaps in a few cases, there is considerable promise for future development." Ten years later Cruse (1959) summarized the economics of utilization of xerophytic plants (including shrubs) and stressed the need for a processing system that will recover all the extractives of value in the plant raw material and, as completely as possible, utilize any byproducts. Again, our survey results are in agreement. The data we have assembled may help identify those shrub groups having the highest incidence of potentially useful raw materials.

Section III.

Genetic Potential

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Evolution and diversity of arid-land shrubs

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Shrubs do not constitute either a taxonomic or an evolutionary category. This fact is basic to any discussion of their evolution. A shrub can be defined as a plant having woody, persistent stems, but no central trunk such as trees have. Given this definition, we readily conclude that shrubs and herbs, as well as shrubs and trees, can exist as alternative genotypes within the same species. A well-known species containing both shrubby and herbaceous races is the castor bean (*Ricinus communis*). Among the numerous species containing both shrubby and arboreal races is the interior live oak of California, *Quercus wislizenii*. The evolution of shrubs from either trees or herbs, and the reverse process, probably occurred many times during the evolutionary history of such a flexible group as the flowering plants.

Directions of evolutionary trends

A review of relationships between genera within many modern familiies supports the hypothesis that shrubs can be derived either from trees or less commonly from herbs. In addition, relatively primitive shrubs may give rise in some instances to trees and in other evolutionary lines to herbs. In predominantly arboreal genera, such as *Acer* and *Quercus*, the shrubby species are probably derived from tree-like ancestors. On the other hand, trees that belong to families containing chiefly shrubs, such as *Oxydendron* (Ericaceae), *Fraxinus* (Oleaceae), and *Triplaris* (Polygonaceae), are likely to have been derived from shrubby ancestors.

The predominant trend from shrubs to herbs is evident in almost every large family. Well-known examples can be cited from the Rosaceae (*Potentilla*), Leguminosae (*Cassia, Sophora, Mimosa*), Euphorbiaceae (*Euphorbia*), Solanaceae (*Solanum*), and Compositae (tribe Heliantheae). Nevertheless, examples can be cited of a trend in the reverse direction, from herbs to shrubs. The most clearly documented of these are certain genera of oceanic islands, such as *Dendroseris* on Juan Fernandez, *Sonchus* and *Echium* on the Canary Islands, *Scaevola* on various islands of the Pacific, and Campanulaceae-Lobelioideae on Hawaii (Carlquist 1966, 1969a, 1969b, 1970). Carlquist explains, on the basis of adaptation, why this reversal of the usual trend might be expected to occur on oceanic islands. He also gives a reasonable hypothesis, based on developmental considerations, of the evolutionary mechanism by which it could be accomplished. Following Darwin, he points out that on oceanic islands, particularly those of volcanic origin, the plants most likely to become established upon the raw soils by means of accidental long-distance dispersal would be hardy, drought-resistant herbs or subshrubs. Plants having these growth forms would therefore be the initial colonizers of such islands. Later, as the soil weathered and became more favorable for plant growth, habitats that could support shrubs or trees would develop. Since natural transport of seeds of already evolved shrubs and trees from distant continental regions would be difficult; with little competition, some of the herbs and subshrubs would evolve into shrubs or trees *in situ*.

The evolutionary mechanism by which this could happen involves the principle of paedomorphosis. Carlquist points out that the specialized wood that is characteristic of the more advanced angiosperms is localized in the secondary vascular tissue. The procambial initials of primary vascular tissue have the long narrow shape characteristic of primitive xylem and phloem cells. In some instances of the reverse evolution from herbaceous species to shrubs, the specialized secondary wood may be retained. In other evolutionary lines, however, the later developmental steps that give rise to such secondary wood may be suppressed, and wood having a more primitive appearance may develop directly from elongated cambial initials.

I believe that the trend of evolution from herbs to shrubs has not been restricted to remote oceanic islands, but has occurred also on larger islands and under special circumstances even in continental floras.

Veronica

An example from a relatively large insular area of a group of shrubs that probably evolved from herbs is the genus *Veronica* (including *Hebe*) in New Zealand. The numerous species of this genus are common and widespread shrubby elements of the New Zealand vegetation. All of them are of polyploid origin, having n=21, 20, or multiples of this number, whereas the herbaceous *Veronica* species of the Northern Hemisphere have chiefly the basic number x=7 (Frankel and Hair 1937). The derivation of the shrubby New Zealand species of this genus from herbaceous or subshrubby ancestors now found in the Northern Hemisphere is, therefore, highly probable.

Mimulus

An example of a similar evolutionary trend in a region that is now continental is found in California, also in the family Scrophulariaceae. The genus *Mimulus* belongs to a tribe that consists almost entirely of herbs, most of them extreme herbs of wet habitats. Within the genus itself, those species that have the least specialized flowers, such as *M. moschatus*, in which the corollas are almost regular, belong in this category. Nevertheless, there exists in California a group of shrubby *Mimulus* species, sometimes placed in the separate genus *Diplacus*. The probable origin of these shrubs from herbaceous ancestors was called to my attention many years ago by the late F. W. Pennell (personal correspondence), a well-known monographer of the family. This example, however, may not contradict the principle developed by Carlquist that the origin of shrubs from herbs is most likely to take place on islands. The shrubby species of *Mimulus* are most abundant and diversified in the coast ranges of California and the neighboring Channel Islands. These regions were continental islands during the middle part of the Tertiary period, which was, most probably, the time when the genus *Mimulus* began its active evolution. Although not volcanic, the islands were subject to great orogenic or mountain-building activity. Because of the gradual desiccation of the climate, with the disappearance of summer rains (Axelrod 1958), small pockets of semiarid climate and desiccated soil must have developed quickly and frequently on these Tertiary islands. In a plastic and genetically rich genus like *Mimulus*, shrubby species suited to such conditions would occasionally be expected to evolve in a direction counter to the usual trend.

Artemisia and the Chenopodiaceae

The example of shrubby *Mimulus* species suggests that the trend from herbs to shrubs may exist also in continental regions. Support may be found in two of the principal groups of shrubby species found in arid regions of the northern hemisphere: the genus *Artemisia* (the sagebrushes) and the various shrubby genera of the Chenopodiaceae, such as *Atriplex*, *Eurotia*, *Grayia*, and *Sarcobatus*.

The genus *Artemisia* is a highly specialized genus of the family Compositae. In a family that has normally insect-pollinated flowers, it has become specialized for wind pollination, with heads (capitulae) much reduced and aggregated into compound inflorescenses. The tribe Anthemidae, to which *Artemisia* belongs, consists principally of herbaceous species. This is true not only of the genera *Chrysanthemum* and *Tanacetum*, less specialized forms which are the nearest relatives of *Artemisia*, but also of three genera, *Hymemopappus*, *Hymenothrix*, and *Leucampyx*, which apparently provide connecting links between the Anthemidae and other tribes of the family, and so must be regarded as among the most primitive members of the tribe. Hence, regardless of whether one believes with Cronquist (1955) that the entire family Compositae was basically and originally herbaceous, or with Carlquist (1966) that the earliest Compositae were shrubs, the evidence suggests that the shrubby species of *Artemisia* are secondary. Hall and Clements (1923) point out that the section *Seriphidium*, which includes most of the shrubby species such as the North American sagebrushes, is relatively specialized in floral characteristics. They suggest that in *Artemisia* the evolution from the herbaceous to the shrubby habit of growth may have taken place in three separate evolutionary lines.

This hypothesis is supported by studies of stem anatomy. Diettert (1938) has shown that the young stem of *Artemisia tridentata*, even when it is well enough developed so that abundant secondary xylem has been formed, still contains a circle of separate bundles, separated by parenchyma, rather than a continuous ring of vascular tissue. An anomalous feature of this species is the formation of layers of cork between the growth rings of xylem (Diettert 1938, Moss 1940). This condition is an adaptation to severe conditions, either cold or drought, and is found chiefly in herbaceous species of various genera. Moss records it in both herbaceous and woody species of *Artemisia*, and points out that only the more specialized species of both herbs and shrubs possess this characteristic.

The woody genera of the Chenopodiaceae share with the herbaceous genera of this family an anatomical characteristic best explained by assuming that the entire family, and several related families, all originated from a common herbaceous stock, which has repeatedly given rise to evolution in the direction of shrubs and even trees (Takhtajan 1959, p. 38). This is the feature of anomalous secondary thickening (Metcalfe and Chalk 1950, p. 1,075). The first-formed vascular bundles may either form a circle of widely separated units, or may be scattered through the stem, giving a superficial resemblance to monocotyledons. Later, concentric zones of collateral vascular bundles arise from a succession of arcs or rings of cambium situated in the pericycle or, occasionally, the phloem. Consequently, the woody stems of such shrubs as saltbush (*Atriplex*), winter fat (*Eurotia*), and greasewood (*Sarcobatus*) do not have the usual dicotyledonous wood structure, consisting of an internal zone of xylem separated by a single ring of cambium from an outer zone of phloem. Instead, they have a series of concentric rings of cambium, each of which has formed its own xylem and phloem. This mode of growth can give rise not only to woody shrubs, but even to thick-stemmed plants that look like trees, such as the saxaul tree (*Haloxylon*), found in the sandy deserts of central Asia.

One might justly ask the question: What selective pressures or other conditions made possible the establishment of this unusual anatomical condition that has caused an entire order of flowering plants to evolve in growth form in an opposite direction from the usual trend? In the examples already given, the reversal was associated with the colonization of island habitats. Could similar conditions have been responsible for the secondary origin of shrubs from herbs in xeromorphic Compositae and Chenopodiaceae?

The conclusion that they probably were is prompted by the evidence presented by Axelrod (1958) and others on climate and plant associations in the early part of the

Tertiary period, when the groups concerned were probably beginning the most active phase of their evolution. At that time, the prevailing climate throughout the northern hemisphere was mesic, with ample rainfall throughout the year, so that continuous forests existed through much of North America and Eurasia. Nevertheless, there were probably "ecological islands" of more xeric climate, resulting from the rain shadows formed by isolated mountain ranges, or from other unusual combinations of ecological conditions. As the overall climate became more arid during the middle of the Tertiary period, these xeric islands increased in size, and new ones probably appeared.

The forest trees and mesic shrubs that formed the "sea" of forest surrounding these islands were already too specialized and rigid in their requirements to be able to give rise to xeric shrubs optimally adapted to the new condition. Notably, few if any of the dominant shrubs found in the arid portions of North America appear to be derived from immediate common ancestors with the woody elements of the neighboring mesic forests. This restriction, and the ease of seed transport and establishment that both now and formerly have been characteristic of families such as the Compositae and Chenopodiaceae, suggest the evolution of xeric shrubs from semixeric herbs in these families. Such a process could take place more quickly and easily than the evolution of xeromorphic adaptations in trees and shrubs belonging to genera such as *Acer*, *Alnus*, *Betula*, *Carya*, *Cornus*, *Fagus*, *Hamamelis*, *Liquidambar*, *Lithocarpus*, deciduous species of *Quercus*, *Salix*, and other inhabitants of the surrounding forests. The evolution of these secondary shrubs is, therefore, a good example of the general principle of evolutionary opportunism.

The origin of monotypic shrubby genera in Tertiary xeric islands

The hypothesis of early Tertiary xeric islands is well supported by another characteristic of the shrubby flora of western North America. Many monotypic or ditypic genera apparently have few or no close relatives, and their phylogenetic origin is highly controversial. Among the best known of these are *Crossosoma* and *Simmondsia*, which represent monotypic families; *Fremontodendron* and *Lyonothamnus*, which occupy anomalous positions in the families to which they are usually assigned; *Carpenteria*, which is the most primitive living member of the Saxifragaceae subf. Hydrangeoideae; and various genera of Rosaceae, such as *Adenostoma*, *Cowania*, and *Purshia*, *Chamaebatia*, *Cercocarpus*, *Coleogyne*, *Fallugia*, and *Vauquelinia*, along with the Mexican genus *Lindleya* and two South American genera, *Kageneckia* and *Quillaja*. A reasonable hypothesis of their taxonomic isolation makes them products of extensive evolution of semixeric shrubs during the upper Cretaceous period, when arid areas were relatively numerous and widespread. With the onset of widespread mesic, equable climates at the beginning of the Tertiary, particularly the Eocene, only the hardiest of these xeric and semixeric forms could survive in specialized ecological islands that provided favorable habitats. I have seen such conditions in the rain forest area of Malaya, where semixeric species are localized on ridges of hard quartzite, and in the mesic forests of western Oregon, where outcrops of hard rock and shallow soil support localized populations of species that occur chiefly in drier regions.

When, during the Oligocene and Miocene periods, more xeric islands appeared and increased in size, those species that had survived the mesic interlude in special situations were now able to spread and in some instances to become very common. Nevertheless, their gene pools had become so much restricted during the long period when they existed only as small populations in refugial areas that they could not become diversified into a series of newly evolved species.

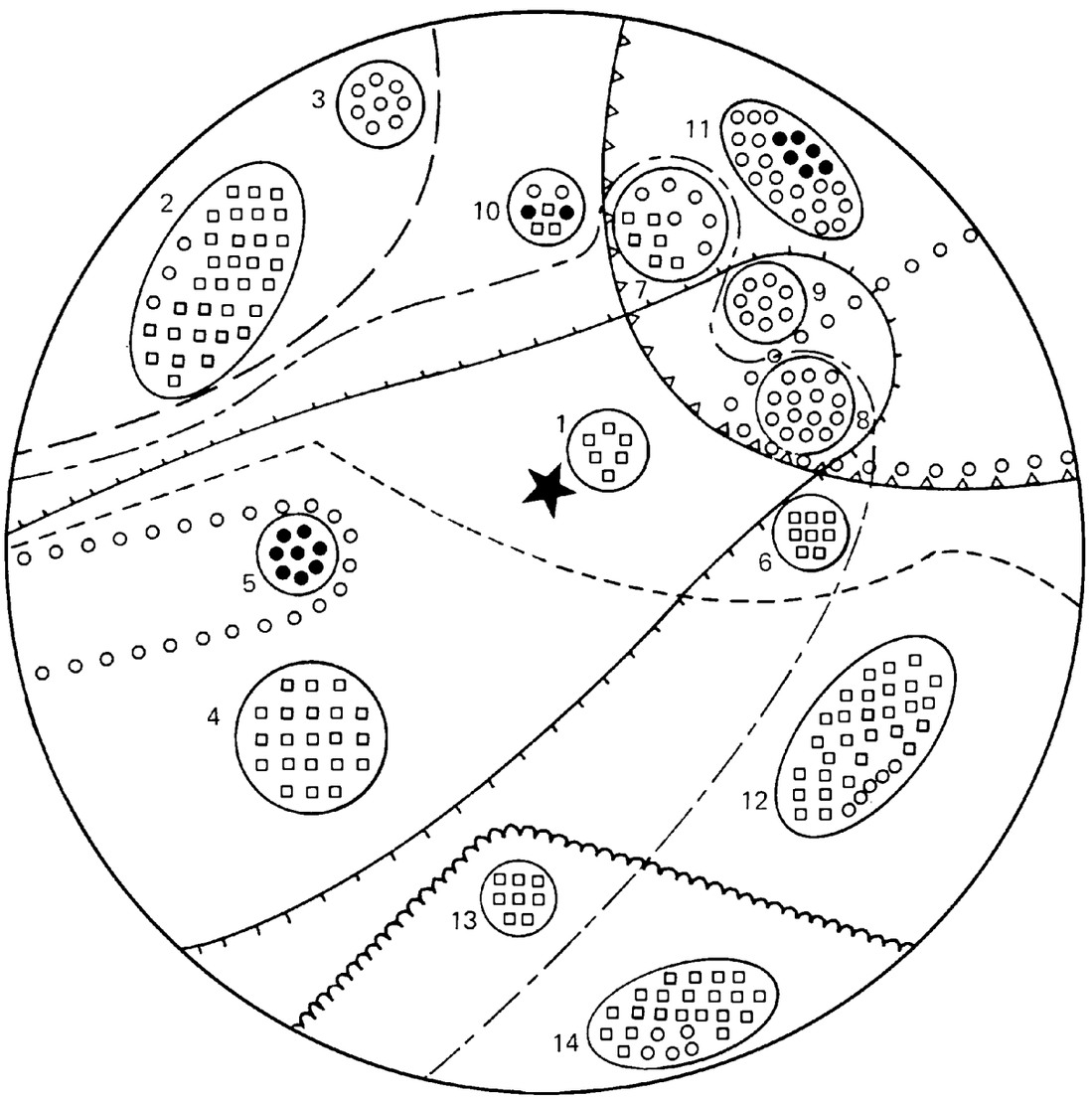
Refugial islands in relation to the origin of large, complex genera

A modification of the principle of refugial ecological islands can explain the evolution of large genera containing many species, such as *Arctostaphylos* and *Ceanothus*. If, during the dominance of the mesic early Tertiary forests, closely related members of the same species had become isolated and separated from each other in different islands, they could be expected to evolve in somewhat different directions. Later, as the islands increased in size, migrations from one to another, or even the coalescence of two different ones, might be expected to occur with increasing frequency. Previously isolated and differentiated races could be brought together, and large gene pools could be assembled by means of hybridization and genetic segregation. Isolates from these new gene pools could colonize the newly available semiarid and arid habitats. In the period of mountain-building activity during the Pliocene, and in the advance and retreat of glaciers and pluvial periods that followed during the Pleistocene, arid and mesic areas oscillated in size and shifted position, and this process has continued up to the present time. In groups that had a sufficiently large gene pool to profit from these oscillations, speciation has gone on continuously, and the operation of the "compound interest law" would ensure the existence of a large number of modern species, even if only a few existed at the beginning of the process.

The evolution of these large, complex shrubby genera is, therefore, an example of the principle of rapid evolution in small, semiisolated populations, first postulated by Sewall Wright, and discussed in many modern books and papers (Stebbins 1950, Ehrendorfer 1951, Grant 1971, Dobzhansky 1970).

On this principle, groups that were actively evolving in the semiarid intermediate zones between mesic forest and truly arid desert would have given rise periodically to more specialized derivatives, some adapted to more mesic and others to more xeric conditions. That such derivatives have evolved is evident from careful analyses of several groups, both woody and herbaceous. I would like to illustrate one of these analyses by means of a device, which I am calling an ecophyletic chart. Before it is constructed, the species of a genus (or in some instances the genera of a family) are rated according to the number of advanced states that they possess with respect to a series of characters for which generalized and advanced or specialized states can safely be postulated on the basis of a careful study of the group itself as well as its relatives. A circle or ellipse representing the group is then placed on the chart at a distance from its center, marked by a star, that corresponds to the number of advanced states that the group possesses. The ecological adaptation or adaptations of the group are represented by conventional symbols similar to those used to identify rock formations on a geological map. Consequently, the chart permits the observer to recognize quickly any associations that may exist between the specialized characters found in a species and the habitat that it occupies. In the chart presented in figure 1, the different characters on which it is based are represented by different kinds of lines, which are explained in the key. In every instance, the species that are found outside of the line possess the specialized state of the character concerned, which is mentioned first in the key. The species that are not separated from the central star by a particular line possess the primitive or unspecialized state with respect to the character that the line represents.

Figure 1 is an ecophyletic chart for the genus *Ceanothus*, subgenus *Euceanothus*. It shows that the least specialized species occupy semixeric habitats, whereas more mesic and more specialized species have originated several times during the evolution of the subgenus. In this particular example, there are relatively few instances of evolution in the direction of greater xerophytism. In a chart of the generally more xeric subgenus *Cerastes* of *Ceanothus*, however, several such trends would become evident. A more extensive use of ecophyletic charts is planned for future publications, including a forthcoming book on trends of evolution in flowering plants.



Mesic woodlands

Mesic, open country

Semixeric woodlands and marginal areas

CEANOTHUS, SUBGENUS CEANOTHUS

Key to Characteristics

- Leaves 3-veined vs. 1-veined
- Flower clusters compound vs. simple
- Flowers blue vs. white
- Leaves deciduous vs. evergreen
- Branches spiny vs. not spiny
- Branches angled (in cross section) vs. not angled
- Plants prostrate vs. erect

Key to Species

1 ochracea
2 buxifolius, cordulatus, depressus, Fendleri, leucodermis
3 incanus
4 dentatus, foliosus, impressus, Lemmonii, papillosus
5 diversifolius
6 spinosus
7 integerrimus, Palmeri
8 microphyllus, serpyllifolius
9 ovatus
10 velutinus
11 americanus, sanguineus, Martinii
12 arboreus, coeruleus, oliganthus, sorediatus, tomentosus
13 Parryi
14 cyaneus, griseus, thyrsiflorus

Figure 1.--Ecophylogenetic cross-sectional chart of Ceanothus, *sect.* Euceanothus

Relationships between shrubs and trees

The same flexibility postulated for the evolution of herbs from shrubs and vice versa is evident in the relationship between shrubs and trees (Stebbins 1965). Theoretical arguments can be presented for both directions of evolution. During an increase in the severity of the climate, particularly a shortening of the growing season and the onset of strong winds, shrubby genotypes could be expected to develop from existing successful arboreal species. Characteristics such as reduced stem growth, a greater ability to proliferate new stems from the root system, and a tendency to grow horizontally rather than vertically would provide the best adaptations to the newly arisen, more severe conditions. On the other hand, during a period when, either locally or throughout the earth, the climate was evolving toward greater equability and more mesic conditions, there would be an opposite tendency. The richness of the gene pools of shrubby species that occupy localized and shifting semiarid habitats would permit them to give rise, from time to time, to vigorous, fecund derivatives capable of occupying niches within climax communities.

The hypothesis that the original angiosperms were shrubby or subshrubby (i.e., semiherbaceous) appears to me now as valid as when it was first advanced (Stebbins 1965). Takhtajan (1970) criticized it on the grounds that no evidence was presented from the most generalized of modern families. Such evidence is very difficult to obtain because these families are relictual; nevertheless, it exists. In the Dilleniaceae, which, for reasons to be advanced elsewhere, I regard as coequal in primitiveness with the Magnoliales, the shrubby genus *Hibbertia* has more primitive wood than arboreal genera such as *Dillenia* (Dickison 1967). The most primitive wood in the Dilleniaceae is found in the arboreal or shrubby genus *Didesmandra* and in *Schumacheria*, which is a woody vine or liana. These genera have highly specialized flowers that resemble those of the more advanced species of *Hibbertia*. Most probably, the three genera have diverged from a common ancestor, a shrub, like the modern species of *Hibbertia* that have the least specialized flowers. In the Winteraceae, the living genera, with one exception, have the high polyploid basic number x=43 (Ehrendorfer and others 1968), and are therefore certainly derived from extinct ancestors of unknown growth habit, having lower chromosome numbers. The only species of Winteraceae having a lower basic number (n=13), those in *Drimys* subg. *Tasmannia*, show specialization in their dioecious flowers and reduced carpel number. They are predominantly shrubs. In the Annonaceae, shrubs and lianas are more frequent than large trees, and there is no clearcut evidence that either shrubs or trees are the more primitive in this family. Finally, in the Magnoliaceae, in which the secondary evolution of shrubs from trees has certainly occurred, a secondary polyploid basic number, x=19, again indicates a complex evolutionary derivation from ancestors now extinct. Although other evidence is lacking, the large size and complex, highly specialized anatomy of the flowers of Magnoliaceae (see review in Skipworth and Philipson 1966) suggest an evolutionary increase in overall size of the plant. The arboreal members of the family could, therefore, be derivatives of extinct shrubby ancestors.

The evolution of the deciduous condition

An evolutionary trend that has occurred repeatedly in many groups of woody plants, both shrubs and trees, is the acquisition of deciduous foliage. Since deciduous trees are most common in high latitudes and are usually associated with long, cold winters, most botanists have assumed that the deciduous habit has been acquired in response to cold. Axelrod (1966) has pointed out, however, that fossil floras of the early Tertiary and the Cretaceous age, when deciduousness most probably evolved, contain a mixture of deciduous and broad-leaved evergreen species, many of the latter having tropical affinities. Such associations could not have tolerated the severe winters now prevailing in regions like the northeastern and central United States, where the greatest concentration of deciduous species among contemporary floras occurs. Axelrod has, therefore, suggested that drought rather than cold has been the principal selective agent in the evolution of the deciduous habit.

The evidence from shrubs that inhabit temperate arid regions supports Axelrod's contention that cold alone cannot have determined deciduousness, but at the same time, works against the idea that drought was the only factor. Sagebrush (*Artemisia tridentata*) and related species of *Artemisia* from central Asia illustrate both of these points very well. They inhabit regions which, for severity of climate, in both drought and cold, are not equaled anywhere else in the world where woody plants can grow. Nevertheless, they have persistent leaves. The same is true of several other genera and species of arid-land, cold-resistant shrubs, such as *Chrysothamnus* and *Atriplex hymenelytra*, although perhaps the majority of them are deciduous.

Observations on the distribution of evergreen and deciduous shrubs and trees in California have led me to a somewhat different hypothesis of the origin of the deciduous habit in the majority of woody plants that inhabit mesic temperate regions. California is favorable for such observations, because its mild temperatures are similar to those that probably prevailed at the time when deciduous angiosperms were first evolving, although its moisture regime, characterized by long dry summers, is very different. Moreover, California contains many evergreen as well as deciduous species, usually growing side by side in different plant associations. Of the 137 species of angiospermous trees and shrubs found in the Coast Ranges of Central California, 76 are evergreen and 61 are deciduous. Central California is climatically marginal. Its coastal strip is essentially frost free, and in its wettest portions adequate moisture is present throughout the year. Its colder interior portions have mild frosts and a growing season of 210 to 240 days, and in its drier sections there is a deficiency of moisture during 5 months of summer.

If drought were the principal environmental factor promoting the deciduous condition, we would expect to find the highest proportion of deciduous species on the hotter, drier slopes of the interior, and the lowest proportion in the moisture regions, regardless of temperature. Such is not the fact. Of the 16 species of deciduous trees, five (*Populus trichocarpa*, *Salix lasiandra*, *S. laevigata*, *Aesculus californica*, *Acer negundo* var. *californica*) are found throughout the region; six (*Populus fremontii*, *Alnus rhombifolia*, *Juglans hindsii*, *Quercus douglasii*, *Q. lobata*, *Fraxinus latifolia*) are absent from the coastal section, but are more or less abundant throughout the interior; two (*Acer macrophyllus*, *Quercus garryana*) are coastal and northern; one (*Quercus kelloggii*) is interior and northern; and one (*Platanus racemosa*) is confined to the southern part. The patterns of distribution of the 45 deciduous shrubby species are somewhat similar.

Two facts should be noted about the species mentioned in the last paragraph. In the first place, a larger number of them occur in the interior but not along the coast as compared to the number that are strictly coastal. The species of the interior are better adapted to the marked differences in temperature between summer and winter that prevail there than to the equable climate found along the coast. In other words, the more continental climate of the interior supports a higher proportion of deciduous species than the more insular climate of the coast. This condition is probably widespread. In the Eastern United States, which has a much more continental climate than the west coast, many deciduous species of trees extend southward to regions having a growing season of up to 240 days. Axelrod (1966) has noted that even in high latitudes there are many fewer deciduous species in the Southern than in the Northern Hemisphere. The reason may well be that the larger proportion of ocean to land in the Southern Hemisphere gives its temperate portions a less continental climate that that of comparable latitudes in the Northern Hemisphere. This suggests that one favorable condition for deciduousness is a continental type of climate, with its fairly strong contrast in temperature, both between winter and summer and between night and day.

An even more striking fact is the concentration of deciduous species along streambanks (table 1). Of the 16 species of deciduous trees, 10 occur entirely or primarily

Table 1.--*Comparison of habitats of deciduous and evergreen species of woody angiosperms in the central coast ranges of California*

Item	Deciduous		Evergreen	
	Chiefly streambanks	Chiefly hill slopes	Chiefly streambanks	Chiefly hill slopes
Trees	10	6	0	7
Shrubs	22	23	0	69
Total	32	29	0	76

in this single rather restricted habitat. Of the remaining six species, two (*Quercus garryana*, *Q. kelloggii*) reach their southern limit in central coastal California, while a third (*Juglans hindsii*) is doubtfully native to the area. The concentration of deciduous shrubs along streambanks is equally striking. In addition to several species of *Salix*, examples are *Calycanthus occidentalis*, *Cercis occidentalis*, *Clematis ligusticifolia*, *Physocarpus capitatus*, *Euonymus occidentalis*, *Cornus glabrata* and *C. californica*, *Rhododendron occidentale*, *Cephalanthus occidentalis*, *Sambucus callicarpa*, and *Baccharis viminea*.

It is significant that none of the 76 evergreen species of angiosperms are confined to streambanks, and only a few, such as *Umbellularia californica*, occur commonly in this habitat. This suggests that in a climate having mild winter frosts and relatively dry summers, the most favorable habitat for the origin of the deciduous condition is a streambank.

These observations should be extended further, particularly to the less arid portions of southern Arizona, southern Texas, and northern Mexico, where light winter frosts occur but where the dry season comes during the cold rather than the warm months. Wooded swamps, marshes, and deltas, habitats which are absent from central California, should also be investigated. At present, however, the following working hypothesis seems justified: The deciduous habit, including particularly the elaboration of genetically conditioned abscission tissue at the base of leaf petioles, originated very often in trees or shrubs inhabiting streambanks or other habitats where the soil is perpetually saturated with moisture. This was particularly likely in a climate having a dry atmosphere and sharp fluctuations in temperature. Such a climate would have had some winter frosts but would still have been mild enough to permit the survival of many species of broad-leaved evergreen angiosperms.

The physiological basis for the hypothesis will be apparent to anyone who has cultivated tender evergreens in a climate having mild frosts. If such plants are heavily watered during the autumn, they are much more likely to be damaged by frost than if they are allowed to harden by withholding of water. Moreover, if the first frost is followed immediately by hot, dry weather, as is likely in a semiarid climate, the damage is more severe than if the frost is followed by a cool, moist spell.

We can imagine, therefore, that in the marginal type of climate described above, woody plants inhabiting streambanks or swamps, with their roots kept perpetually moist, would be much more susceptible to frost damage than those growing on the drier hillsides. This damage would be particularly severe in a semiarid, continental climate, in which daily fluctuations of temperature would be great, and the dry atmosphere would be poorly insulated against the heat. Since the streambank habitat is otherwise very favorable for woody plants, we might expect there a maximum selection pressure in favor of genetically-controlled mechanisms, such as leaf abscission, that would protect the plant against frost damage.

The hypothesis postulates, therefore, that the chief basis for the origin of the deciduous condition in mesic trees and shrubs of temperate regions was the selective advantage that this condition provided in hardening the plants prior to the onset of frosts. This selection pressure would have been exerted most strongly on plants inhabiting streambanks and other sites having moisture-saturated soils, because these would not have been subject to hardening by drought.

Conclusions

This brief review should serve to show that shrubs may provide answers to a number of problems in the evolution of flowering plants. Plants having this growth habit may have been characteristic of the earliest angiosperms. During more recent evolutionary history, they have given rise to more specialized descendants, both herbaceous and arboreal. At the same time, particularly in severe climates, the evolution of shrubs from trees as well as from herbs has taken place repeatedly. Shrubs exemplify more than any other kinds of plants the great plasticity that has been largely responsible for the outstanding evolutionary success achieved by flowering plants. The deciduous condition in both shrubs and trees has been evolved under the influence of a continuously moist habitat in a climate having mild frosts and fluctuations of temperature.

Selection

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There are several modes of plant selection, but today we will consider them under two categories--natural and artificial. I mention them here merely for background consideration. The first is as old as the plant kingdom, and the second is probably as old as when man began to cultivate plants for his own improved food supplies.

Natural selection is the process by which plant species and subspecies have evolved in nature and become adapted to their habitats. Population types created by natural selection and adapted to local habitats are called ecotypes. There may be many ecotypes within a species or subspecies, each adapted to a local climatic or edaphic condition. There are often important differences in characteristics between ecotypes, but interhybridization is common (Clausen, Keck, and Hiesey 1940, 1945). Variations within ecotypes may be called races or biotypes. I will have more to say later about the phases of natural selection and its possible importance in improvement of shrubs for wildland sites.

Artificial selection is the picking out of certain variants from populations for superior attributes as they would relate to a particular purpose, and the propagation of them, either vegetatively or through progeny. In horticultural practices, highly superior individuals may be propagated vegetatively, or the selections may be propagated through seed for extended crossing and further selection. The former is often resorted to for trees and shrubs bearing superior nuts and fruit. For instance, Hale peaches result from a seedling selected for having a highly desirable fruit. It has been propagated widely through grafting and budding. Some superior woody plants are propagated by planting rooted clones. This has been resorted to in the development of some seed orchards of hardwood forest trees (Rudolf and others 1971). Also this technique is used for increasing trees and shrubs in the horticultural trade.

For many thousands of years men have been selecting superior progeny of all classes of horticultural plants to meet a wide range of sites and climates. The origin of some plants was prior to the dawn of history; the origin of others is shrouded in obscurity. Actually, we do not know the progenitors of corn (*Zea mays*) which had its origin on the American continent (Vavilov 1951).

It is uncertain how long selection by man remained incidental, without any known relation to heredity, and how soon it was consciously performed. One of the earliest known cultivated plants was date palm, grown by the ancient Babylonians and Assyrians. Babylonian hymns recite 360 uses for the plant. The date palm has the sexes separate, that is, in different trees. Consequently, plants raised from seeds of the same tree, no doubt, differed greatly among themselves; the Babylonians likely witnessed and considered this variability and selected them for improved dates. It is known that rice has been cultivated in the Orient for more than 50 centuries. Ancient writings of the Chinese show that deliberate preservation of the best seeds and their use in propagation were practiced. Aristotle, who lived in the fourth century before Christ,

recognized crossing as a means of obtaining knowledge of heredity. Consequently, much of what is sometimes regarded as new truly is not.

Mass selection

Artificial selection is possible because related individuals in similar environments exhibit similar and dissimilar attributes which are hereditary characters. When these appear, we can incorporate or eliminate them in the succeeding generations by appropriate selection and breeding practices. When a conspicuously advantageous new character appears, selection may be employed to preserve individuals exhibiting it and these individuals may then be used for further propagation. Often, a new character may at first be only faintly pronounced, such as a slight difference in the degree of expression already present in the stock. This new character may appear as a slightly larger or better fruit, a more vigorous seedling, more tolerance to freezing temperatures, or the ability to persist on a drier soil site.

Good discernment and sound judgment are necessary to make the most of selection and there usually must be an adequate objective. The selector must be able to define his aim and discriminate between fine differences. In the absence of any precise method of assessing the kind or degree of improvement, there is no good substitute for astute judgment acquired by experience. Early selectors probably preserved the more valuable individuals and eliminated the less valuable ones without any thought of altering the general characteristics of the population. No doubt, this was the type of selection used in the development of many plants and animals in prehistoric times. Methodical selection, as used today, is the conscious and deliberate practice of modifying the general character of the stock according to some predetermined standard. This is accomplished by making a careful choice of certain individuals for the parents of the next generation and by controlling the breeding of these individuals. The individuals for further breeding are determined by (1) appearance, (2) record of ancestry, and (3) record of progeny. Remarkable results have been obtained by this more modern mass selection approach.

By using pure line selection we can produce progeny that exhibit the same genotype. A pure line strain can be developed by increasing self-fertilized progeny from a single, true-breeding plant. Assuming that the plant originally selected is homozygous for all gene pairs, the progeny should be alike, except for differences caused by environment or mutation. The making of selections involves various improvement programs of species and is a sophisticated procedure. I do not believe this is the place to enter into a discussion regarding these selection techniques as our knowledge regarding wildland shrubs is too preliminary for their use. Also, we lack background details for an accurate prescription of best selection; however, there are some helpful ways in which we can improve our planting stock.

Discern and classify

We probably can follow the example of people who work in forest tree improvement. Perhaps we can go as far as they have and classify seed-producing areas of important shrub species for habitats and uses. We could even classify seed-producing areas in nature as plus, almost plus, normal, and minus, just as the tree improvement people have done for some trees (Rudolf and others 1971). We could then specify that seeds be harvested from the plus and almost plus areas, as they do. These procedures have resulted in some notable improvement of progeny when compared to progeny from the general run of trees. Certainly, we must consider selection of seeds of shrubs for specific purposes such as production, palatability, erosion control, and landscaping. In Utah, we have made some classification of antelope bitterbrush (*Purshia tridentata*) seed-producing areas and noted them as producing upright, medium upright, and decumbent layering ecotypes. We have established seed-producing orchards of certain ecotypes of bitterbrush and fourwing saltbush (*Atriplex canescens*), and vasey big sagebrush (*Artemisia tridentata vaseyana*).

In our present effort in Utah, we can see good opportunity for classification in the assembling of geographic ecotypes we have made for the study of growth and reproductive characteristics under similar conditions of climate and soils. These collections exhibit striking differences between subspecies and ecotypes in their comparative adaptation to a common site. They also furnish a gene pool for preliminary selection and breeding. As we acquire more information, we can classify seed-producing areas in nature more widely and wisely. We hope to plant seed-producing orchards of superior ecotypes.

Luther Burbank, the most widely acclaimed producer of horticultural plants in America, was breeding and selecting plants in the early part of this century. He was a tremendously discerning observer, and despite unsophisticated techniques, had a genius for picking good progenitors. To a considerable degree, his success resulted from the fact that he assembled large numbers of closely related species, subspecies, and genera. These served him well as a gene pool, although he did not call it this. However, his success can primarily be attributed to his ability to see significant utilitarian characteristics in plants. He was ever alert to find even minute characters that would serve as clues to the ultimate improved value of the plant.

It has been pointed out that Burbank did not create new characters (Howard 1946). He merely brought forth recombinations of behavior that had previously existed, either in the parents or some of their ancestors. I give the matter some emphasis because to make important improvement in shrubs for wildlands, I believe scientists must have, or develop, this ability to see traits meriting propagation. Lack of this ability is a major shortcoming even in many well-trained men.

In this Symposium today, we are discussing shrubs for wildland uses and, to some extent, their possible improvement and development through selection and breeding. We are more fortunate than Luther Burbank and his contemporaries because we have an infinitely greater background of technology on which to rely. As I have indicated, the laboratories for improvement of forest trees probably can give us some rather direct help. The selection of wildland shrubs is essentially a virgin field, and from the great many variations we see in nature, I am sure there are some tremendous accomplishments to be made even if we do no more than follow the selection techniques of Burbank. Variants of many species of shrubs already exist in nature and are available for our programs. First we must recognize the important ones that will serve as progenitors and then bring them together for evaluation and development. Although making improvements and determining adaptations of plants to the more severe site conditions of wildlands present more problems and require more time than doing the same for cultivated crops, there is no reason why notable improvement cannot be made.

The shrubland complex

There are considerably more than 800 million acres in North America where woody perennials either occur as some important part of the cover or actually characterize it. Probably most of this area is west of the Mississippi River where many shrubby formations can be quite readily recognized. There are several ways to classify them. I have grouped them as follows, along with their approximate estimated acreages:

	Acreage (Million)
Sagebrush and associated northern desert shrubs	245
Juniper-pinyon	75
Mountainbrush	15
Salt-desert shrub	70
Southern desert shrub	360
Chaparral	30

These are composite totals, and each is comprised of several species. Details regarding their variation in composition are available in other publications, therefore I will not discuss them here.

Shrubs occur over nearly the full gamut of types of climate and soil. They may be found at all altitudinal and latitudinal limits, except where the ground is permanently covered with snow. They are the prevailing cover in the hot deserts below sea level in the Salton Sea basin and in Death Valley (Benson and Darrow 1944). Shrubs are immensely valuable for stabilization of soils which would otherwise be completely barren because of constant subjection to wind and water erosion.

Some rationale has grown up, at least in western America, that some woody plants are "bad" and others are "good" because of their differences in aggressiveness, forage value, susceptibility to fire, water consumption, and other attributes. No doubt, considerable bias has developed as to what may be "good" or "bad" shrubs. Some that may be "good" in certain environments are considered "bad" in other environments. Outstanding examples of this are the widely occurring big sagebrush *(Artemisia tridentata)* and rubber rabbitbrush *(Chrysothamnus nauseosus)*. A large number of mechanical and herbicidal techniques have been devised for importantly reducing or eliminating them because of some belief that these plants are not contributing importantly enough. However, on many winter ranges for livestock and big game, these shrubs are important sources of forage. Because of their high nutritive value (Esplin and others 1937, and Cook and others 1954) and the fact that in this season they are palatable as well as highly productive, they have been recommended for seeding and improvement of extensive winter game ranges in Utah. Because of their rapid growth and good attributes of reproduction they are probably the best shrubs available for this purpose. Special effort has been directed to aerial planting of them on large blocks in Utah (Plummer and others 1968). Despite their merits, many land managers steadfastly resist their inclusion for elements of browse. Actually, there are no plants which are all "bad" or all "good." It is likely that this resistance has resulted from the fact that many valuable ecotypes and biotypes have been all but eliminated by selective grazing.

As we look ahead to the planting of shrubs on rangeland, we must consider species, subspecies, ecotypes, and biotypes, both native and exotic, for specific purposes such as cover for wildlife, food for game and livestock, protection and beautification of recreation areas, roadsides, and disturbed landscapes.

Habitat variation

Heavy grazing by livestock and big game over the past one-and-a-quarter centuries has been responsible for reducing, and in some instances markedly opening, closed stands of shrubs and grasses on extensive areas in the West. Some of the other uses related to man's activities, of course, had sharper and quicker effects than grazing but their impacts have not been so continuous, nor have they affected such large areas. Important among them are clearing of land for crops, mining (and associated industry), roadbuilding, harvesting of trees, and greater incidence of fire. Regardless of how the opening of closed communities resulted, it has made a great many sites available for increase of shrubs. That many openings are still persisting is quickly recognized by rapid occupancy of them by annuals. The prevalent ones in the Intermountain area are Russian thistle *(Salsola kali tenuifolia)*, halogeton *(Halogeton glomeratus)*, and cheatgrass brome *(Bromus tectorum)*. It is interesting that these annuals are all exotics. Annuals are gradually replaced by perennials including shrubs.

The opening of closed communities of herbs and shrubs has provided habitats for the establishment of new innovations and creations resulting from nature's combinations of closely related species and ecotypes. Edgar Anderson (1948 and 1953) calls this "the hybridization of the habitat." It is a good characterization. Openings

have made possible an important increase of ecotypes and biotypes through introgressive hybridization and natural selection. Many of these former openings provide excellent places from which to make selections for specific purposes.

In addition to recent opening of communities by the hand of man, the much slower forces of climatic change and the natural erosion associated with it over many thousands of years have, no doubt, also been responsible for creating conditions which increase variations in shrubs. Cottam, Tucker, and Drobnick (1959) found climatic changes were important in affecting the structure of oakbrush communities in a change from a cool to a warm climate between 7,500 and 4,500 years ago in Utah. In this warm postpluvial period, Gambel oak *(Quercus gambelii)* and turbinella oak *(Q. turbinella)* apparently existed together in north-central Utah. In a subsequent cooling period, turbinella oak did not survive and receded to the warmer temperatures of southern Utah to which it was accustomed, and where it was more at home with its true chaparral associates. That it was once present more than 260 miles north of where it now occurs is evidenced by F-1 hybrids and some backcrosses that survived cooler temperatures. In its warmer climate of southern Utah and northern Arizona, turbinella oak is associated with Gambel oak over a wide range where similar hybrids and backcrosses are found in abundance, some of them of recent origin. These same crosses have been artificially made and validated by Cottam and his associates. Since established hybrids can spread and maintain themselves by root sprouting, they persist indefinitely. No doubt, some clumps have an age of at least a few thousand years.

Stutz and Thomas (1964) have pointed out the possibility of cliffrose *(Cowania stansburiana mexicana)* and antelope bitterbrush *(Purshia tridentata)* having been historically together in Montana and Idaho and having hybridized as they do where they grow together in Utah. Cliffrose may have been lost due to subsequent cooling of the temperature, but its introgressed glandular characteristics in the leaves were retained in the more cold-tolerant bitterbrush.

While looking for good shrubs as parents for improving game ranges in Utah, we have seen what appears to be abundant incidence of polyploidy and introgressive hybridization between ecotypes (Anderson 1953, and Stebbins 1960). Wherever the species of mahogany occur together or have been together, the putative hybrids are found. Noteworthy intermediates are seen in leaf size and structure of the shrubs; this has been particularly noted in the hybridization of true mountain mahogany *(Cercocarpus montanus)* with curlleaf mahogany *(C. ledifolius)* and littleleaf mahogany *(C. ledifolius* var. *intricatus)*. That the generally desirable trait of fire tolerance has been transmitted from true mountain mahogany to the hybrid is attested by its occurrence on fire scars from which curlleaf has been completely lost. Many of these hybrids produce viable seed. They often exhibit the attributes of both parents, and in some ways are superior to both. The same can be said for antelope bitterbrush and fourwing saltbush and their hybridization with closely related species and ecotypes. In the case of these shrubs we have confirmed by artificial crossing what we have observed in nature.

Big sagebrush subspecies and many ecotypes and biotypes present tremendously impressive variation (Hall and Clements 1923; Ward 1953; Beetle 1960; and Plummer and others 1968). From what I see, I would say we need to give more emphasis to improvement of palatability in ecotypes of this shrub rather than perhaps to its widespread elimination. Particularly wide variation has been noted in the palatability between ecotypes of big sagebrush as well as between subspecies. Likely, the differences are related to the chemistry and amount of essential oils in the various ecotypes. A simple two-dimensional phenolic extraction on chromatography paper proved useful for quickly separating palatable from unpalatable ecotypes (Hanks and others 1971). While there is little likelihood that phenols making the patterns and colored spots on the paper are responsible for the palatability or the lack of it, excellent association was found between these and observed palatability. This simple laboratory procedure was successfully utilized to quickly predetermine palatability of sagebrush ecotypes and biotypes.

The technique appears to have usefulness for other species of shrubs. Holbo and Monzingo (1965) successfully used chromatography to segregate species and subspecies in the Tridentatae.

Certainly, it is clear that introgressive hybridization, both sympatric and allopatric, has and is continuing to have a tremendous effect on the gene flow from ecotype to ecotype and even from species to species and sometimes between genera that are closely related. Other genera in addition to *Artemisia* within which there is immense expression of hybridization, no doubt followed by backcrossing which results in widespread diversification and opportunities for selection, are *Atriplex, Amelanchier, Ceanothus, Cercocarpus, Chrysothamnus, Ephedra, Eurotia, Purshia, Quercus, Ribes,* and *Sambucus*. Much needs to be done to authenticate by artificial means what we can see in nature and then develop the avenues for improvement.

Another important element giving rise to stimulation of gene flow is that the centers of diversification and origin of a number of the shrub genera and species are in the Western United States. Consequently, there are more species and ecotypes of shrubs assembled here from which to make selections than probably anywhere else in the world. For this reason alone, there is a greater amount of inherent variation in the germ plasm than found elsewhere. This, along with habitat openings for establishment, importantly maximizes the chances for the creation of new shrubs for wildlands. I am impressed that this potentially creative aspect is highly active. The fact that a great many natural hybrids between closely related species have been observed gives credence to this (Rowntree 1939; Clausen, Keck, and Hiesey 1940, 1945; Hanson 1962; Cruise 1964; Drobnick and Plummer 1966; Plummer and others 1957, 1968). Further, successful artificial hybridization between several closely related species substantiates what has been observed in nature (Drobnick and Plummer 1966). Some of these have become fairly well stabilized as in the reported instance of desert bitterbrush *(Purshia glandulosa)* (Plummer and others 1957; Stutz and Thomas 1964).

Plant introduction stations

In addition to this assembly of shrub ecotypes in Utah, which we plan to expand to other States having different soils and climates, the four organized Agricultural Research Service Plant Introduction Stations are an important aid in assembling germ plasm of shrubs by plant explorations throughout the world. They occur in four different climatic areas: Experiment, Georgia; Geneva, New York; Ames, Iowa; and Pullman, Washington. The Pullman, Washington, Station has recently undertaken a fairly intensive program at the Central Ferry Site near the Snake River for assembling native and foreign accessions of shrubs as they have been doing over the past 25 years for many other classes of plants. This growing collection will provide a place for assessing and selecting from a large array of plants that will probably have usefulness for varying site conditions in many western States. In building this collection, they will be looking for source materials from any and all who would send them to Pullman. Collections will be there for examination and, to some extent, small amounts of seed will be produced and can be supplied to cooperators. I mention this because it can be an important aid in selecting and developing better shrubs.

Consequently, there are many opportunities for discovering and creating improved shrubs for a multiplicity of purposes. Indeed, there is rich opportunity to select from a large assortment of shrubs which nature has provided. Given guidance, the chances are excellent for improvement of shrubs for wildlands through selection and breeding. The time has arrived when we should give strong impetus to this research.

Cytology and cytogenetics of shrubs

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Chromosomes are cell organelles formed of nucleic acids, particularly DNA, and protein. The exact fine structure of the chromosome is not known, but it is generally thought to be formed of a core of DNA (and some RNA) surrounded by a jacket of nucleoprotein. The strands of nucleic acid can twist and bend during cell division in an as yet unknown way to form the chromosome that is visible during metaphase.

The DNA present in the chromosome carries the genetic information necessary for the orderly development and function of the organism and the cell that contains it. This function is discharged by the decoding of appropriate messages for the manufacture of specific enzymes, at specified and exact moments in the development of the cell and individual. Regulation of gene action is the primary function of the chromosome. However, for a normal functioning of the organism and to assure continuity of the species, chromosomes, and the genetic codes they contain, must be transmitted in an orderly and precise manner from cell to cell, and from parent to offspring. Exact and precise self-replication during interphase followed by orderly separation of the products of division in mitosis or meiosis is a second major function of the chromosome.

A third role of chromosomes, that of regulating gene recombination, is less direct. In effect, because each chromosome contains more than one gene, the law of independent assortment is not truly operative for the genes in a chromosome. The fewer chromosomes an organism has, the more the number of linked genes, and the greater the deviations from independent assortment exhibited by the progeny. This phenomenon of chromosome number and its evolutionary implications are set forth in this paper, with particular relation to the shrubby habit.

The genetic system

The law of independent assortment states that genes that are not linked (that is, are in different chromosomes) will assort during meiosis independently, following the laws of probability. So, for example, given two independent loci, each heterozygous for a pair of alleles, A_1 A_2 and B_1 B_2, and given that the probability of any of them going to one or the other pole during the first division of meiosis is exactly one-half, the probability of one product of meiosis containing both A_1 and B_1 is therefore the product of their probabilities, that is, $0.5 \times 0.5 = 0.25$. With three alleles, it would be $0.5 \times 0.5 \times 0.5 = 0.125$ and so on, so that for n loci it is $(1/2)^n$. Under independent assortment, gametes will contain a complement of alleles that are a random sample of each of the pairs present in the parental genotype. In turn, if mating were truly random, the offspring formed by the random mating of two such gametes would be a random sample of the genes present in the parental generation.

If genes were independent of each other in function, formation of offspring by random sampling of the parent generation would be an efficient method. However, genes are not independent in function and certain combinations of alleles are optimal and

others deleterious. A mechanism that maintains intact optimal combinations of genes and prevents others from forming is therefore selectively advantageous over random assortment. Packing of genes in individual chromosomes so that they can be transmitted as a unit is such a system, and it is advantageous for evolution.

However, the situation is further complicated. Although certain gene combinations are optimal and others deleterious at any one time, the optimal combination at one time is not necessarily optimal at a later time. This is because both the physical and biological environments are constantly changing. There is no way for the organism to predict the direction and intensity of the environmental change; consequently its response is accommodation through natural selection when change occurs.

Recombination is the mechanism that reassorts the genes in each generation. It is the result of the interaction of a series of phenomena. According to the genetic system (Grant 1958; Solbrig 1970), the biological factors that affect recombination in plants are:

1. Chromosome number
2. Average number of chiasma per chromosome
3. Generation length
4. Population size
5. Breeding system (gene flow within populations)
6. Incompatibility system
7. Gene flow between populations
8. Crossability barriers and external isolating mechanisms (gene flow between species)

Recombination is the major source of immediate variation in the population. Because genes are carried on chromosomes, recombination is restricted: the fewer the number of chromosomes, the greater the restrictive effect. However, the genes on a chromosome are not completely linked. They can separate through genetic exchanges between chromatids of homologous chromosomes, the phenomenon of crossing-over. The frequency of crossing-over, or at least its physical manifestation, the frequency of chiasma, varies from species to species. The greater that frequency, the higher the proportion of recombination gametes produced during meiosis. Chiasma diminishes the effect of a finite number of chromosomes and increases recombination.

The number of recombinant types among the offspring of a plant population is given by the formula

$$\frac{r\,(r+1)}{2}^{n}$$

where r = average number of alleles at a locus and n = number of independent loci. Because of linkage, the formula is not readily applicable, but it can be seen that if there is no crossing-over, and if we consider that there are at least five different mutant forms for each chromosome, a population of a species having 10 chromosomes would produce 15^{10} different kinds of gametes!

The number of recombinants in a unit of time (e.g., 1 year) is obtained by multiplying the number of recombinants by the number of generations (N) in a year:

$$\frac{r\,(r+1)}{2}^{n} \times N$$

Other factors being equal, a plant that produces two generations a year will produce twice as many recombinants as a plant producing only one generation a year. The length

of generation has another important effect: not all the offspring will survive to adulthood. In a natural situation where populations are in equilibrium, usually called "climax" vegetation, on the average the number of seedlings surviving is roughly equivalent to the number of organisms dying. If the species is long lived, the rate of turnover is slow. But long-lived organisms have a chance of producing many more offspring in their lifetime than short-lived ones. It follows, then, that a much smaller proportion of the offspring of a long-lived organism survives to adulthood than that in a short-lived one.

The larger the population, the greater the possibility of storing genetic variability. In the extreme case of a population formed by two organisms, there can be at most four different alleles for each gene and there is a potential of forming by sexual reproduction 10 different combinations for each gene in the following generations. In a population with three organisms, there is a maximum of six alleles for each gene in the population and a potential of forming 21 different combinations; with four individuals, eight alleles and 36 combinations, and so on. With n individuals, there can be a maximum of $2n$ alleles and a potential of forming $(2n \times n) + n$ recombinants. This figure is of course a maximum estimate that is never realized, and is based on the *effective* breeding population size. But it serves to illustrate the effect of population size.

Any breeding system that promotes outbreeding increases the effective breeding population size and consequently affects potential variation in the population. The same can be said of any mechanism that promotes gene exchange between breeding populations (such as seed-dispersal mechanisms, or long-range pollen vectors). But because different breeding populations are presumably subjected to different selection pressures, gametes introduced from neighboring populations have a higher probability of carrying unique alleles than gametes from the same population. Consequently, crosses between populations usually contribute more towards increasing recombination than crosses between members of the same breeding population. This principle applies particularly to crosses between related species, provided there are no sterility considerations.

Summarizing this brief introduction to the genetic system, recombination, that is, the independent assortment of the allelic genes in the offspring, is the major source of new genotypes in the population, and the major source of unique phenotypes on which natural selection acts. However, the theoretical maximum potential of recombination is never attained, because of several constraints imposed on the process of recombination. First (and most important), genes are carried on chromosomes; this limits independent assortment to genes in different chromosomes, although crossing-over within a chromosome pair allows partial recombination between linked genes. Furthermore, a number of other population characteristics restrict recombination even further; there are primarily population size, breeding system, and length of generation.

Because some of these characteristics vary and are under genetic control (at least in part), natural selection is able to act on them to control the amount of recombination. But the extent to which selection acts on each of the components of the genetic system varies. This imposes a constraint on the evolution of recombination systems. Presumably for every population at any one ecological situation in time, there is an ideal amount of recombination that maximizes the genetic potential of the species. Through natural selection the population tends to approach that ideal level.

The ecological situation

Plant environments differ in many characteristics. If all aspects of the environment are considered, almost every plant grows in a unique microenvironment. Because seeds are dispersed, the offspring of a particular individual always grows in a microhabitat slightly different from that occupied by the parent. But even an established

plant does not face the same habitat all the time because of the climate. In other words, the habitat varies in space and in time. Every individual plant has to cope with variation in time throughout its life, and the offspring faces variation in space at the time it is dispersed. Natural selection acting on populations of offspring in space and in time tends to select that combination of phenotypes that can best cope with environmental changes in time and produce offspring that also can cope with variation in space.

Presumably an environment that is completely invariant in space and in time would tend to select the *one* phenotype (and underlying genotype) best adapted to those conditions. A population faced with such an environment would tend to become monomorphic, that is, formed by genetically and morphologically identical individuals. On the other hand, an environment that oscillates in time (as with the seasons), but not in space, would call for a phenotype that could adapt to these changes in time. Alternatively, it would call for a phenotype that could produce, with every oscillation in time, offspring adapted to the new situation. Another strategy would be development of a phenotype that could live in one environment and survive in a passive state (e.g., as a seed) through the unfavorable environments.

An environment that changes in space but not in time would call for a series of phenotypes, one for each of the various environments in space. Each phenotype would either produce offspring like themselves or produce more than one kind of offspring, each adapted to one of the environments. Which of these two strategies was selected would depend on the area and distribution of the various environments, that is, on the predictability of the environment that the offspring faced.

But environments vary in both space and time, and furthermore, their predictability also varies. Consequently, plants must be able to produce phenotypes that adapt to the changes in time and must also be capable of producing a variable offspring. More than one allele at each of several loci, followed by recombination, assures the production of a variable offspring. How much variability exists in the offspring, measured as the dispersal around the population mean (coefficient of variability) depends on the number of segregating loci, the gene frequency of the various alleles in the population, population size, breeding system, and other factors. Evidence is also accumulating that seems to indicate that individuals with many heterozygous loci tend to be more plastic; that is, they are able to adapt to more environments in time than more homozygous individuals can.

We find, then, a rather complex situation. On the one hand, at each generation, selection eliminates from the population all those individuals (and their genes) that find themselves unable to cope with the physical and biotic components of the environment in which they germinate. Presumably, selection also favors the more heterozygous individuals. On the other hand, because of the spatial variation in microhabitat selection, it also favors populations capable of producing more than one kind of offspring. How much variation exists depends on the underlying system of recombination.

Habit and chromosome number

The various components of the genetic system and the forces that control them are set forth in table 1. Only habit and chromosome number are considered here.

A species is usually classed as annual, biennial, or perennial. The longer its life span, the more variability is found in the lifetime of individual members of the species. Generation length is an adaptation to the ecological situation. The milder the physical environment, the greater the percentage of long-lived species in that flora. Annuals, on the other hand, are found usually in oscillating environments, such as deserts (where the "wet season" comes and goes) or in disturbed sites (where the

Table 1.--*Components of the genetic system, their variability and controls*

Genetic system component	Variability	Control
Chromosome number	Nearly invariable	Strong stabilizing selection
Chiasma frequency	Mildly variable	Under direct genetic control
Generation length	Invariable to mildly variable	Environmental and genetical control
Population size	Fairly variable	Determined by environment and density factors
Breeding system	Fairly invariable	Genetic control
Incompatibility system	Fairly invariable	Genetic control
Gene flow	Variable	Indirect genetic control
Crossability barriers and external isolating mechanisms	Variable	Indirect genetic control

disturbance is temporary and followed by periods of no disturbance). An annual usually occupies a relatively uniform environment, which is only temporarily available (in space, in time, or both). A perennial, on the other hand, occupies an environment that is much more widely available in space and time, but which is also more variable. On this basis, annuals should be less variable than perennials, and consequently should have a lower recombination index. The lower recombination index should reflect itself (statistically at least) in all the elements of the genetic system. If the foregoing argument is correct, species of annuals as a group should have fewer chromosomes than species of perennials.

It should be remembered, however, that the number of chromosomes is only one element of the genetic system and that we are dealing with a finely tuned mechanism. Consequently, within each phyletic line we should expect different balances between chromosome number and size, chiasma frequency, breeding system, and other characteristics. By looking at various phyletic groups, we should be able to discover these different balances.

Chromosome number and habit in Compositae and Leguminosae

The ideas just set forth were tested on the large families Leguminosae and Compositae. Information from Fedorov's index and from the various indexes of chromosome numbers of plants by Cave, Ornduff, Moore, and others is the basis for tables 2 through 5 and figures 1 and 2. The Leguminosae and Compositae were selected because they are large families and well known cytologically, and they differ from each other in areas

Table 2.--*Chromosome number in species of Leguminosae by habit*

Chromosome number	Annual herbs		Perennial herbs		Shrubs		Trees		Total	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
5	12	4.7	8	1.5	--	--	--	--	20	2.0
6	32	12.5	34	6.2	2	1.2	2	3.8	70	6.9
7	88	34.5	85	15.6	6	3.7	--	--	179	17.6
8	38	14.9	187	34.3	20	12.3	2	3.8	247	24.2
9	1	0.4	10	1.8	3	1.8	1	1.9	15	1.5
10	5	1.9	17	3.1	14	8.6	3	5.8	39	3.8
11	14	5.5	58	10.6	3	1.8	2	3.8	77	7.6
12	7	2.7	16	2.9	10	6.1	2	3.8	35	3.4
13	--	--	5	0.9	14	7.4	15	26.9	34	3.3
14	7	2.7	40	7.3	11	6.7	17	32.7	75	7.4
15	3	1.2	2	0.4	3	1.8	--	--	8	0.8
16	16	6.3	31	5.7	13	7.9	--	--	60	5.9
17	--	--	--	--	--	--	--	--	--	--
18	3	1.2	6	1.1	1	0.6	--	--	10	1.0
19	1	0.4	--	--	--	--	--	--	1	0.1
20	10	3.9	5	0.9	3	1.8	1	1.9	19	1.9
Over 20	18	7.1	41	7.5	62	38.0	9	17.3	130	12.8
Total	255	100.0	545	100.0	165	100.0	54	100.0	1,019	100.0

Table 3.--*Chromosome number in species of the subfamily Papilionoideae*

Chromosome number	Annual herbs		Perennial herbs		Shrubs		Trees		Total	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
5	12	4.7	8	1.5	--	--	--	--	20	2.2
6	32	12.6	34	6.4	2	1.5	2	12.5	70	7.5
7	88	34.7	85	16.1	6	4.6	--	--	179	12.3
8	37	14.6	187	35.4	20	15.3	2	12.5	246	26.5
9	1	0.4	10	1.9	3	2.3	1	6.3	15	1.6
10	5	2.0	17	3.2	14	10.6	3	18.8	39	4.2
11	14	5.5	57	10.8	3	2.3	2	12.5	76	8.2
12	7	2.8	13	2.5	8	6.1	--	--	28	3.0
13	--	--	3	0.6	--	--	--	--	3	0.3
14	7	2.8	29	5.5	--	--	--	--	36	3.9
15	3	1.2	2	0.4	3	2.3	--	--	8	0.9
16	16	6.3	31	5.9	13	9.9	--	--	60	6.5
17	--	--	--	--	--	--	--	--	--	--
18	3	1.2	6	1.2	1	0.8	--	--	10	1.1
19	1	0.4	--	--	--	--	--	--	1	0.1
20	10	3.9	5	0.9	3	2.3	1	6.3	19	2.1
Over 20	18	7.1	41	7.8	55	42.0	5	31.3	119	12.8
Total	254	100.0	528	100.0	131	100.0	16	100.0	929	100.0

Table 4.--*Chromosome number of species of the subfamilies Mimosoideae and Caesalpinioideae*

Chromosome number	Annual herbs		Perennial herbs		Shrubs		Trees		Total	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
8	1	100.0	--	--	--	--	--	--	1	1.1
9	--	--	--	--	--	--	--	--	--	--
10	--	--	--	--	--	--	--	--	--	--
11	--	--	1	5.8	--	--	--	--	1	1.1
12	--	--	3	17.6	2	6.3	2	5.3	7	8.0
13	--	--	2	11.8	12	37.5	15	39.4	29	33.0
14	--	--	11	64.7	11	34.3	17	44.7	39	44.3
Over 20	--	--	--	--	7	21.9	4	10.5	11	12.5
Total	1	100.0	17	100.0	32	100.0	38	100.0	88	100.0

Table 5.--*Chromosome number of species of Compositae by habit*

Chromosome number	Annual herbs		Perennial herbs		Shrubs		Total	
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
2	1	0.1	--	--	--	--	1	0.001
3	15	1.9	4	0.17	--	--	19	0.5
4	59	7.8	66	2.81	--	--	125	3.6
5	53	6.9	36	1.5	12	3.2	101	2.9
6	42	5.5	49	2.1	8	2.1	99	2.9
7	50	6.6	63	2.7	1	0.3	114	3.2
8	59	7.8	105	4.5	5	1.3	169	4.8
9	122	16.1	455	19.4	107	28.6	684	19.5
10	44	5.8	139	5.9	26	6.9	209	5.9
11	34	4.5	42	1.8	7	1.9	83	2.4
12	46	6.1	84	3.6	21	5.6	151	4.3
13	14	1.8	68	2.9	8	2.1	90	2.6
14	32	4.2	55	2.3	6	1.6	93	2.6
15	17	2.2	50	2.1	14	3.7	81	2.3
16	24	3.2	32	1.4	16	4.2	72	2.0
17	28	3.7	125	5.3	18	4.8	171	4.9
18	71	9.3	197	8.4	33	8.8	301	8.6
19	6	0.8	44	1.9	5	1.3	55	1.6
20	20	2.6	126	5.4	19	5.1	165	4.7
Over 20	23	3.0	640	27.3	68	18.2	731	20.8
Total	760	100.0	2,380	100.0	374	100.0	3,514	100.0

pertinent to our study. The Leguminosae are a relatively ancient family of tropical origin no later than early Tertiary. Many of its members, particularly in the tribes Caesalpinoideae and Mimosoideae, are trees or shrubs. The Compositae, on the other hand, are a very evolved, relatively young family whose fossil record does not extend beyond the Miocene. Many species are suffrutescent shrubs, but there are very few truly woody species in the family. Furthermore, the family is rare in tropical regions, but highly developed in temperate and cold regions and in mountains. Any correlation between habit and chromosome number found in both these families is good indication of a true trend regardless of evolutionary history. Another advantage of choosing these families is that the number of species for which chromosome counts are available is very large: 1,015 species of Leguminosae and 3,514 species of Compositae were used in this survey. Such large numbers of species make it possible to work directly with species rather than genera; the species are a more natural unit in this case.

Table 2 and figure 1 give the chromosome number of species of Leguminosae by habit. The lowest number for the family is n=5 found in 20 species of herbs, all belonging to the more advanced tribe Papilionoideae (table 3). Twelve of these species were annuals. Species with n=6 are more numerous but are found only among Papilionoideae. Of 70 species with n=6, only two are shrubs and two are trees; the other 66 are herbaceous. The number n=7 is the most common among annual herbaceous Leguminosae, being found in 88 species, representing 34.5 percent of all annual Leguminosae. The most common number in the family is n=8 (more than 20 percent of all counted species of Leguminosae have n=8). Almost three-quarters of the species with n=8 are perennial herbs, 15.3 percent are annual herbs, and 8.9 percent are shrubs and

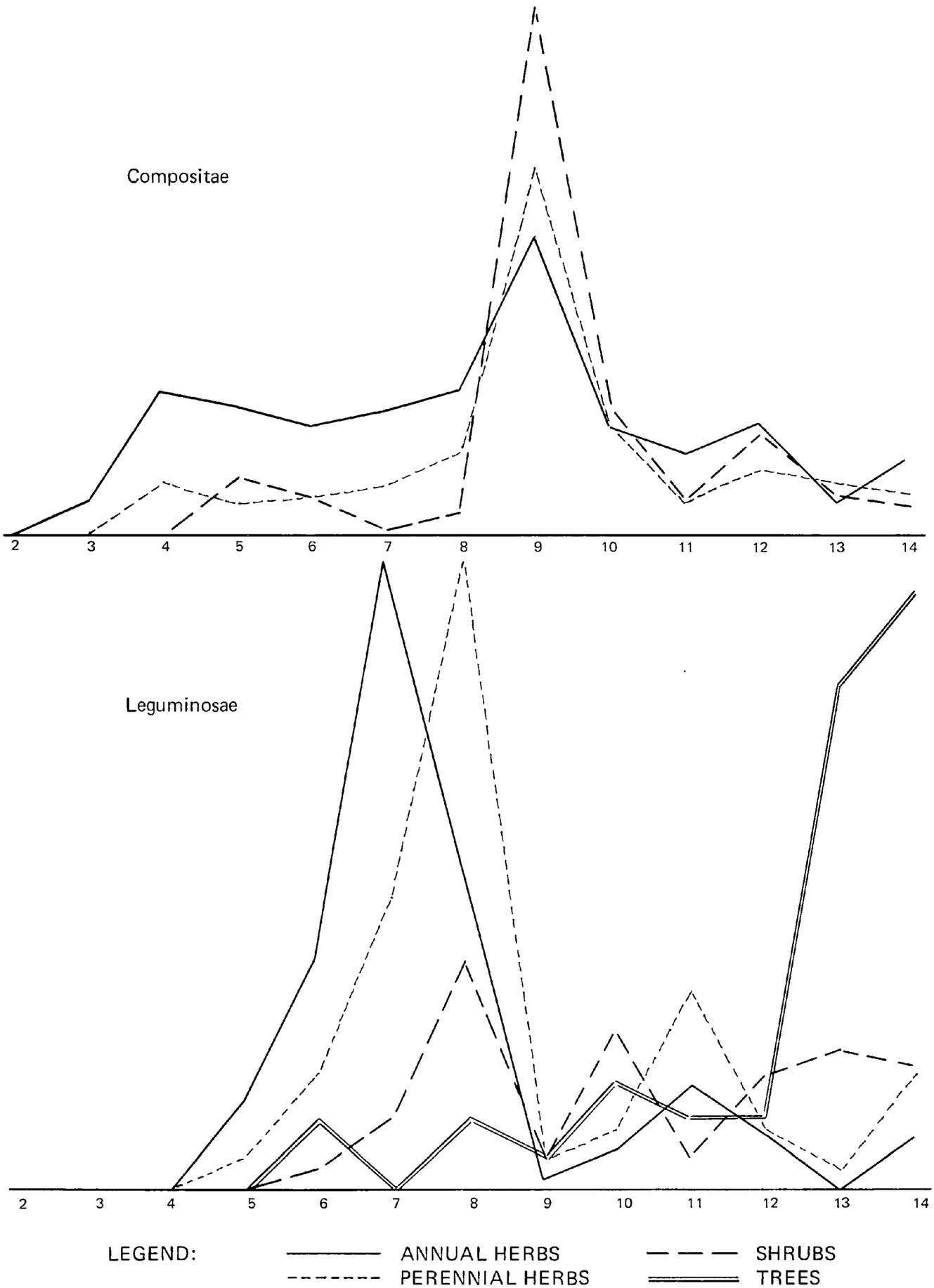


Figure 1.--Frequency of species with different chromosome numbers by habit in Compositae and Leguminosae.

trees. Since half of all the species of Leguminosae counted to date are perennial herbs, 25 percent annuals and 25 percent shrubs and trees, we can see that both groups are underrepresented at the n=8 level at the expense of the perennial herbs. But while the annual species are overrepresented at levels below n=8, the trees and shrubs are more abundant at higher chromosome number levels. This applies particularly to the shrubs.

As to the difference between the subfamilies of Leguminosae, little definite can be said because most counts in the family come from members of Papilionoideae. Counts from the Caesalpinoideae and Mimosoideae (table 4) are all n=11, 12, 13, and 14, with only one exception, n=8, in *Cassia fasciculata*, out of 89 species considered in both these tribes.

The pattern of Compositae (table 5) is similar. One species, *Haplopappus gracilis*, an annual herb from the southwestern United States, has only two gametic chromosomes. This is the lowest count recorded to date in the angiosperms. Numbers n=3 and n=4 are also restricted to herbaceous plants: 15 annuals and four perennial herbs have n=3, and 59 annual and 66 perennial shrubs have n=4. In shrubs of the family Compositae, n=5 is the lowest chromosome number; 12 shrubby species have that number, plus 53 species of annuals and 36 of perennial herbs. The same pattern, that is, a predominance of herbs (particularly annuals) with a scarcity of shrubs, is observed as well for species with chromosome numbers of n=6, 7, and 8. The pattern is reversed for species with n=9, presumed to be the basic chromosome number in the family (Raven and others 1960; Solbrig and others 1963). Of 675 species of Compositae recorded as having n=9, 107 are shrubs (28.6 percent of all shrubs in the family); 122 are annual (16.1 percent of all annuals); and 455 are perennial herbs (19.4 percent of all perennial herbs). At the n=9 level, shrubs are overrepresented while annual herbs are underrepresented, the reverse of the pattern at levels below n=9. Annual herbs with chromosome numbers of n=10 and higher are relatively rare, whereas perennial herbs and shrubs with these higher numbers are not.

In the various tribes of the Compositae, the same trends can be observed (fig. 2). The annual species tend to have statistically lower chromosome numbers than the perennial herbs, and these in turn tend to have a lower chromosome number than the shrubs and trees. However, the exact number and the model number for each habit in each tribe vary greatly. Thus, in the Heliantheae, two species of annual herbs have only three pairs of chromosomes; a majority has from six to 12 pairs. In the Cichorieae, the low number among annuals is also n=3, but a majority of annual species has fewer than nine pairs of chromosomes. Likewise in the Astereae, about half of the annual species have fewer than nine pairs of chromosomes, but 30 percent have n=9.

In brief, the study seems to confirm the hypothesis that annuals have a lower chromosome number than perennials; but since selection is acting on the recombination system and only indirectly on chromosome number, each phyletic line reaches a slightly different adjustment between number of chromosomes, habit, and the various other components of the genetic system.

Chromosome number in shrubs

For the purpose of this discussion, shrubs do not differ from trees. Whenever environmental resources are abundant, vegetation is dense and the perennial elements develop in size and height so as to gain access to sunlight without being shaded. This results in the evolution of the tree habit. On the other hand, when vegetation is sparse because of lack of resources, the perennial elements evolve into shrubs. Cytologically, shrubs and trees as a group should not differ from each other significantly, but they should tend to have a higher number of chromosomes than herbs. Tables 2 through 5 confirm these predictions.

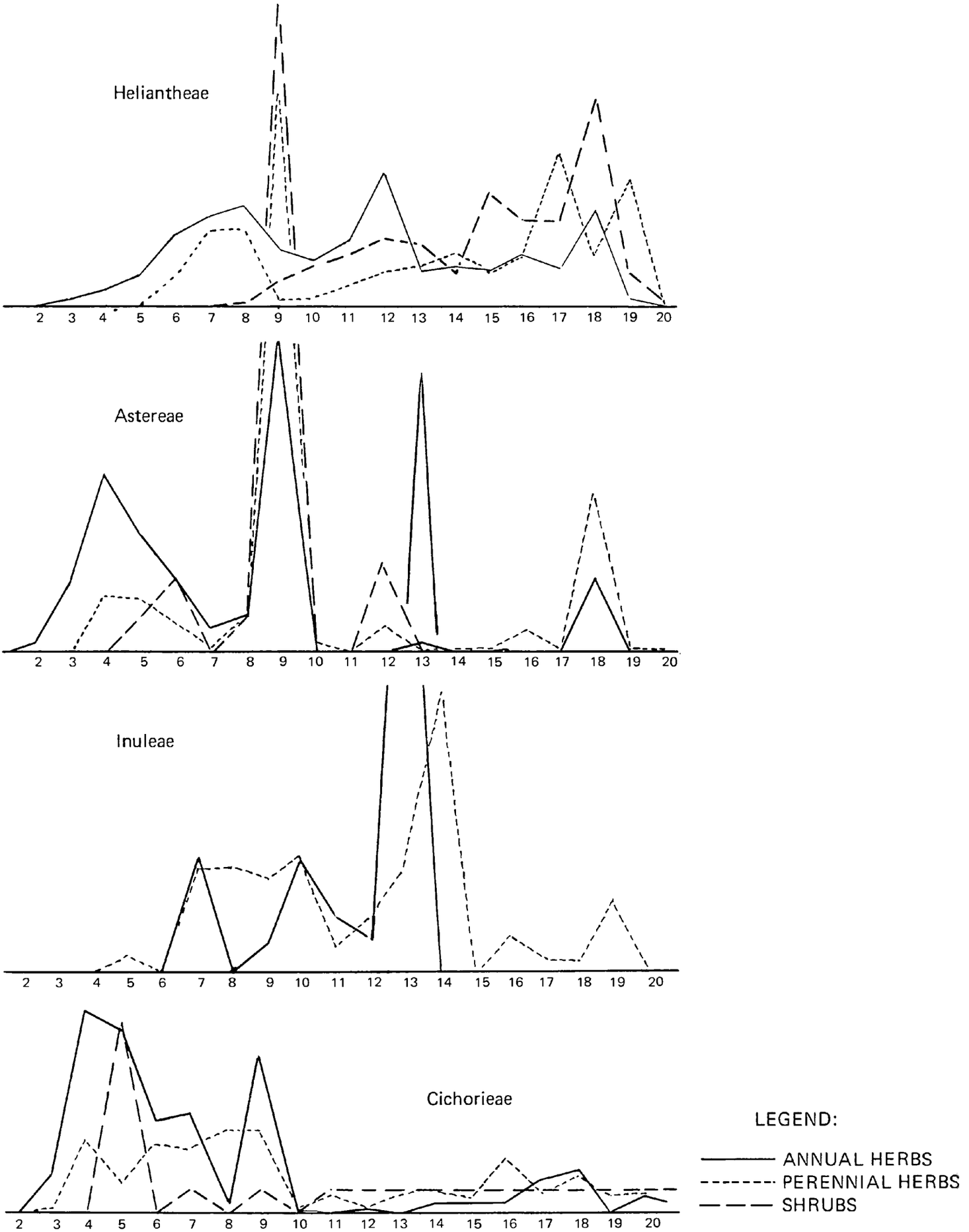


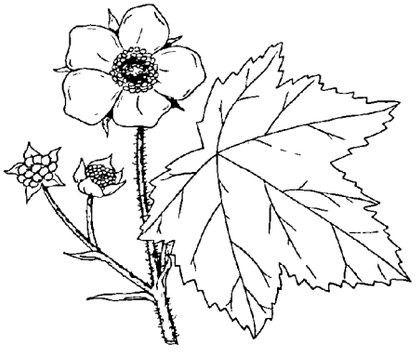
Figure 2.--Frequency of species with different chromosome numbers by habit in four selected tribes of Compositae.

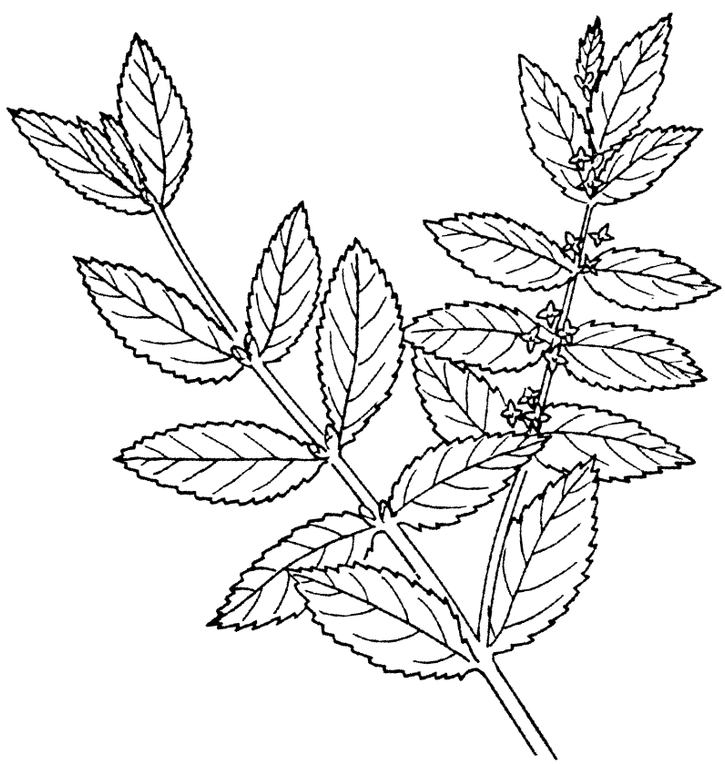
Polyploidy seems to be quite abundant among shrubs. It is the easiest mechanism available to a species for increasing the number of chromosomes. But polyploidy does not increase recombination in the same way that an increase of chromosomes by aneuploidy does, because the linkage groups remain intact. On the contrary, because of tetrasomic inheritance in tetraploids, the linkage may become tighter rather than looser. The explanation for a high percentage of polyploidy is different, at least in part, from the explanation for a low chromosome number in annuals (Stebbins 1950, 1971).

Conclusions

Our survey of the chromosome numbers of species of Compositae and Leguminosae confirmed the predictions about habit and chromosome number. Stebbins (1938) similarly surveyed the basic chromosome numbers of 378 genera of assorted angiosperms and came to a similar conclusion regarding habit and basic chromosome number of the woody genera by the polyploid origin of many of them. In this paper the unit compared has been the species rather than the genus; hence no strict comparison with Stebbins' conclusions can be made. Here, a relatively larger proportion of species of woody genera were found to be polyploid. This may be connected with the distribution of species in genera: a few large genera with polyploid species could account for the observed difference. The restriction of the present survey to Compositae and Leguminosae may bias the results. Stebbins' survey dealt with a much smaller sample than mine.

The present survey indicates that in the Leguminosae and Compositae (and by extrapolation in all angiosperms as well) there is a correlation between habit and chromosome number. In any sufficiently large random sample of phylogenetic line, species of annual herbs have the lowest average chromosome number followed by perennial herbs, while woody species (shrubs and trees) will have the highest number. If different phylogenetic groups are compared, the mean numbers will vary, but the hierarchical arrangement just described will stand. Possibly, this is because successive generations of annuals occupy environments that are more similar than those occupied by successive generations of long-lived perennials.





Genetic improvement in crop species as contrasted with possibilities in shrubs

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All crop and animal improvement is accomplished by the very processes that bring forth new species and modify already existing species in nature. Our task in breeding programs is therefore essentially one of accelerating these evolutionary processes. In short-lived species, such acceleration permits rapid genetic turnover, but in long-lived species, such as shrubs and trees, significant results come much more slowly. This is why most genetic principles have been discovered in short-lived organisms, and also why they have received major attention in breeding programs. In recent years, however, much information has accumulated on the evolutionary processes to which shrubs respond, making possible the design of breeding programs that can yield significant genetic improvement.

The three principal avenues of evolution for better adaptation to environmental assaults are: (1) New mutations; (2) genetic recombination from interspecific hybrids; and (3) polyploidy.

These processes have been demonstrated to be operative in shrubs in nature and therefore offer the greatest promise for shrub improvement.

New mutations

Careful examination of any living species reveals a constant accumulation of new mutations. Most new mutations are immediately harmful and seldom become incorporated in the species, but the process of mutation offers, in time, opportunity for both divergence and improvement.

The potential of new mutations is strikingly illustrated by *Secale cereale* L. (cultivated rye). During the past two decades in the grass nursery at Brigham Young University, in a relatively small population, mutations have occurred in nearly every part of the plant. One mutation increases the number of spikelets at each node of the spike from two to three or more (Stutz 1962). Another mutation causes the plants to grow prostrate on the ground. Two separate mutations cause dwarfing; one by reducing the number of nodes in the stem, the other by reducing the internodal length. Other mutations cause the heads to proliferate and the culms to branch. There are now available so many different mutations in cultivated rye that almost any conceivable theme could be concocted, ranging from giant, bushy plants, 8 feet tall, to dwarf, frail, sterile ones. Even a new species could be prepared with distinctive morphological features and reproductive isolation from its relatives.

Such a rich supply of mutations is apparently available to all known species. Mutation appears to have been directly responsible for the explosive appearance of hawthorn (*Crataegus* L.) during recent years in Eastern United States. According to Brown (1910), between the years 1896 and 1910, 866 new species and 18 varieties of hawthorns were described in North America. Today there are so many different themes of hawthorns, particularly throughout Eastern United States, that no attempt can be

made to name them all. The most likely explanation for this sudden emergence of myriads of new species is that man's agricultural practices have opened up numerous new habitats that previously nonadaptive mutations have suddenly found to be favorable.

By a process less spectacular, but probably of even greater evolutionary significance, new mutations might also bring about genetic improvement by way of genetic assimilation. This appears to have been involved in the origin of divergent species of mountain mahogany (*Cercocarpus* H.B.K.) in the Intermountain West.

As pointed out by Pyrah (1964) several lines of evidence suggest that leather-leaf mountain mahogany (*C. ledifolius* Nutt.) is ancestral to both needle-leaf mountain mahogany (*C. intricatus* S. Wats.) and birch-leaf mountain mahogany (*C. montanus* Raf.). The divergence of these two species from *C. ledifolius* probably came about by genetic assimilation.

Cercocarpus ledifolius, a large evergreen shrub, is fairly common throughout the Intermountain Western United States at elevations of about 7,000 feet. *C. montanus*, a broad-leafed deciduous shrub, usually grows at lower elevations and in more mesic sites throughout Utah, Colorado, southern Wyoming, northern Arizona and northern New Mexico. *C. intricatus* is a small shrub having narrow, needlelike evergreen leaves. It is usually found on ledges of sheer cliffs and other xeric sites almost entirely confined to the State of Utah, extending only slightly into neighboring States.

Individual plants of *C. ledifolius* often exhibit considerable plasticity. During favorable growing conditions, leaves often grow much larger than during dry, unfavorable conditions. Such plasticity is apparently adaptive in the mountain brush zone to which *C. ledifolius* is usually confined, but would probably be quite deleterious in sites characterized by long intermittent periods of drought. On such sites, broad leaves produced during favorable growing conditions might be a distinct disadvantage when it was drier. In such circumstances, plants that tended to produce smaller leaves even under lush growing conditions would probably compete more successfully than those more responsive to environmental fluctuations. Consequently, mutations that increased the frequency at which narrow leaves were produced on each plant would probably accumulate. Conceivably, *C. intricatus* is the product of such genetic assimilation. It now appears to be so fixed in its genetic control of leaf size that even when chance permits it to grow in more mesic sites, it continues to produce only needlelike leaves. I have seen stray plants growing on a streambank bearing needles uniformly not much larger than those on plants growing on the dry ledges above.

This same process of genetic assimilation might have been responsible for the origin of *C. montanus*, which, because of its broad deciduous leaves, is able to compete favorably in more mesic sites with such species as *Amelanchier alnifolia* Nutt., *Prunus melanocarpa* Sarg., and *Quercus gambelii* Nutt. Plants having evergreen leaves sufficiently reduced in size to endure the xeric winter conditions in this environment are probably no match for deciduous species having more extensive leaf surface. Because *C. ledifolius* plants are sufficiently plastic to produce rather broad leaves under favorable circumstances, the broad leaves of *C. montanus* could have been derived from this source by a continuing long-range selection for increased leaf surface.

The disjunct expression of deciduous versus evergreen "leaves," however, suggests that this characteristic is due to a relatively small number of genes and probably began as a single genetic event. In F_1 hybrids between *C. montanus* and *C. ledifolius*, the "evergreen" leaves usually persist for 2 years or less, but the plants are highly susceptible to frost and drought and often show 50 percent or more dieback each winter.

Hybrids often form between *C. ledifolius* and *C. montanus* and between *C. ledifolius* and *C. intricatus*, but hybrids between *C. intricatus* and *C. ledifolius* are extremely

rare. These interspecific hybrids usually exhibit considerably more plasticity than their parents; this suggests that the delicate genetic control of within-penetrance of leaf size and shape is easily disturbed in interspecific hybrids. This might explain why few segregants from these F_1 hybrids are to be found.

A similar disturbance of modifier systems for control of within-penetrance is shown in hybrids between species of pinyon pine. *Pinus edulis* Engelm. growing eastward from central Utah normally has two needles per fascicle. *Pinus monophylla* Torr. and Frem. growing westward from central Utah normally has a single needle per fascicle. In many places throughout central Utah these two species meet and hybridize. The hybrids often have one, two, three, and even four needles per fascicle on the same tree. Such released control of penetrance does not appear to have yet furnished anything of value to pinyon pine but, given an ecological niche or even some human-directed selection pressure, new themes could conceivably be easily extracted.

Like all other species, shrubs appear, therefore, to be subject to new mutations and often profit considerably from them. For genetic improvement of shrubs by way of new mutations, we might, therefore, profitably furnish them either with accelerated mutation rates through application of mutagenic agents or with accelerated selective pressures, or both. The potential is there. All we need to do is design ways of extracting improved themes at a rate sufficiently rapid to make it economically profitable.

Genetic recombination

Interspecific hybridization brings together contrasting supplies of genetic variables that have already been selected and refined into adaptive patterns. Thus they offer far greater opportunities for new valuable combinations than can be derived from the tedious process of screening new mutations. It is not surprising, therefore, that this is the most productive avenue for speciation as well as for crop improvement.

The rich potential provided by interspecific hybridization in shrubs is well illustrated by the hybrids between *Cowania stansburyana* Torr. (cliffrose) and *Purshia tridentata* (Pursh.) DC. (bitterbrush) (Stutz and Thomas 1964). These two rosaceous shrubs are so strikingly different that they have been assigned taxonomically to separate genera. We were able to detect 23 different characteristics that distinguished these two species and there are probably scores of other more subtle differences.

Cliffrose is a fairly large shrub, often growing up to 12 or 15 feet. It grows on somewhat xeric sites throughout Utah southward all the way into Old Mexico. It does not grow north of Utah. Bitterbrush is a much smaller plant restricted to more mesic sites throughout Utah northward through Idaho, Washington, Oregon, and southern British Columbia. It does not grow much south of Utah.

Thus, the entire State of Utah is an overlap area for these two distinctive species. Ordinarily, bitterbrush flowers earlier than cliffrose; therefore, the species remain reproductively isolated. But when bitterbrush is growing on a north-facing slope of a ravine and cliffrose is growing on the adjacent south-facing slope, bitterbrush is often sufficiently retarded and cliffrose sufficiently advanced to permit their flowering periods to overlap and hybridization to occur. F_1 hybrids are fertile and usually backcross onto bitterbrush. So common is such hybridization and backcrossing that essentially no population of bitterbrush in Utah is free of introgression from cliffrose.

For the most part, cliffrose and bitterbrush are well adapted to their habitats throughout Utah, so the products of hybridization and introgression form only a minor component of the native populations. But because of the extensive genetic differences these two species possess, the backcrosses and segregating populations contain a tremendous potential for exploiting any new habitats that might become available.

At the southern limits of the distribution of bitterbrush, one of the recombinant themes has already found an adaptive niche. *Purshia glandulosa* Curran (glandular bitterbrush) appears to be a direct product of bitterbrush-cliffrose hybrids. It is well adapted to the drier, hotter environments of northern Arizona and New Mexico and southern Nevada. Each population is fairly constant for those characteristics that define it as *P. glandulosa,* but each contains other variable characteristics that appear to have been carried along fortuitously from the parental species.

North of Utah, another adaptive theme appears to be emerging, although it has not yet precipitated as a distinct species. Certain populations of bitterbrush throughout Idaho, Washington, and Oregon have been observed to be more palatable than others to sheep. Over the years, various explanations have been offered, but apparently it is simply the result of genetic introgression from *Cowania*. Because *Cowania* is far less palatable than bitterbrush, any plants that possess genes for lower palatability from *Cowania* would be expected to have a distinct advantage over normal noncontaminated plants in areas intensively grazed by sheep. Such a severe selection differential would accelerate greatly the rate of gene flow from *Cowania* into these northern populations of bitterbrush, which is probably the reason why no population of bitterbrush in these areas has been found completely devoid of *Cowania* genes. Sometimes only one or two plants in a population show evidence of genetic introgression, but given such a distinct advantage over normal sister plants, those having the genes of *Cowania* that make them unpalatable can be expected to become ever more prevalent. It may not take long under such accelerated pressure to derive even a separate successful species.

It seems significant that from the thousands of themes that could be derived from the recombination products of *Cowania* X *Purshia*, only two (plus others not yet detected) have found an adaptive environmental niche. Because man can provide a host of other environmental niches (as demonstrated by our agricultural accomplishments) the opportunities for selecting out other adaptive themes from this rich genetic pool appear almost unlimited.

Although the backcross and segregating populations from interspecific hybridization offer the greatest opportunity for formulating new adaptive combinations, F_1 hybrids often exhibit heterotic advantages that are so much superior to both the parents and to any segregating progeny that only the F_1 hybrid itself and segregants very similar to it are all that endure. This appears true not only for some cultivated crops, but also for many native plants, including several shrubs.

As shown by Cottam and others (1959), hybrid oaks (*Quercus gambelii* Nutt. X *Q. turbinella* Greene) discovered along a narrow zone in the Wasatch and Oquirrh Mountains of northern Utah are probably relicts left behind after *Q. turbinella* was eliminated from these areas during the recent postluvial cooling period in the Great Basin. Although these hybrid oaks are fertile, and garden-grown segregants are vigorous, very few plants except F_1 hybrids or near-F_1 hybrids are found in nature. Apparently the heterotic F_1 hybrid theme is the only one that can persist in this narrow restrictive habitat.

Shrub improvement by way of interspecific hybridization appears, therefore, to be a very profitable endeavor. It has proven so in nature; it will almost certainly prove more so with human manipulation. We can bring together in our gardens contrasting parents that may never have come together in nature; we can preserve even weak F_1 hybrids long enough to provide a bridge for genetic introgression; we can provide niches for increasing a variety of themes; and we can intensify selection pressures such as drought, differential grazing, and soil conditions so that the scope of selection for adaptive themes can be greatly extended. The future looks bright indeed for genetic improvement of shrubs by the productive avenue of interspecific hybridization.

Polyploidy

Although, as pointed out by Stebbins (1950), polyploidy is less common among woody plants than among herbaceous perennials, some shrubs appear to have used polyploidy extensively in their evolution. For the most part, these have been such plants as *Rubus*, *Salix*, and *Betula*, which like herbaceous perennials, have unusual facility for asexual propagation. This greatly extends the opportunity for polyploid tissue to become reproductive.

The morphological alternations, such as increased cell size and gigas features, that commonly attend polyploidization are usually not sufficiently adaptive by themselves to give a host plant any significant advantage. Consequently, autopolyploids are less common in nature than are allopolyploids, which have the additional advantage of fixing high fertility in heterotic F_1 hybrids.

An exciting example, however, in which the morphological and physiological effects of autopolyploidy appear to have provided a new adaptive theme in a unique habitat is found in *Atriplex canescens* (Pursh Nutt. (fourwing saltbush). The diploid form of this desert shrub is common throughout areas of alkaline soil of the Great Basin. It is a fairly palatable plant.

Growing in the sand dunes of central Utah near Jericho is a giant form of *Atriplex canescens*. It often grows to 8 or 10 feet and sometimes even up to 12 and 15 feet. Under uniform garden conditions, it has nearly twice the growth rate of normal plants. The gigas habit appears to give it a distinct advantage in the shifting sand dunes to which it is confined. Its giant utricles, its high capacity for layering, and the capacity for its roots to form shoot sprouts all appear to increase adaptation to the sand dune habitat.

Melby[1] has tentatively established the giant form as an autotetraploid variety of *Atriplex canescens*. How many of the adaptive features are direct products of polyploidization and how many have been acquired secondarily is not yet known, but apparently the polyploid event itself was instrumental in initiating many of the new adaptive features. Since there are other sand dunes in Utah not yet inhabited by the giant form, its origin must have been fairly recent. This suggests that most of the adaptive characteristics were probably supplied all at the same time by polyploidization.

It seems strange that such a new polyploid could have become established in a dioecious species, such as *Atriplex canescens*, but Melby has found sex determination in these plants to be highly plastic, and many plants bear both staminate and pistillate flowers even on the same branch. Consequently, the opportunity for sexually perpetuating a polyploid product is higher than might be expected.

Utilization of polyploidy in genetic improvement is, therefore, almost as promising for shrubs as for herbaceous plants. Many examples of interspecific hybrids in shrubs have been recorded; synthetic allopolyploids should therefore be fairly easy to derive, particularly among those that can be propagated vegetatively. Also, since autopolyploidy can be induced with equal or perhaps greater facility, other new adaptive themes by this route might also be attained.

The future for genetic improvement of shrubs seems unusually bright. Many species have already been shown to respond to the very same forces for speciation and improvement that have proven so fruitful in cultivated-crop production. Therefore, deliberate planned breeding programs designed to speed up natural evolutionary processes cannot fail to provide many new and exciting improvements among the already existing shrubs of the world.

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[1]J. R. Melby. A cytogenetic study of a giant from of *Atriplex canescens*. (Unpub.)

Origins and variation in ornamental shrubs

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Shrubs are widely used in landscaping. They require less care and attention than herbaceous plants, and the lower outlines of houses today require shrubs and low trees for proper scale. The breeding and improvement of woody ornamental shrubs is one of the promising undeveloped frontiers of plant science. As we shall see, most ornamental shrubs used today represent the initial stages of plant selection and breeding. Few of the shrubs in current nursery lists have a complicated pedigree. Many of them were species introduced without selection or hybridization.

Currently, nurserymen are showing great interest in finding and putting on the market superior forms of the common garden shrubs. It is now possible to obtain legal protection for the production and sale of selected cultivars of shrubs and other plants capable of vegetative propagation. The law allows patenting of plants and sale of trademarks. Obviously, a plant must be sold in sufficient quantities to justify the cost of either patents or trademarks. The great variety of shrubs available tends to hinder efforts to improve a particular species. Virtually all nurseries are interested in growing and introducing superior plant forms. High overhead costs, however, tend to limit the length of the lists that can be produced and sold economically. Keeping the plants available over considerable periods of time is also difficult. Old horticultural magazines and plant catalogs often reveal plant forms that are no longer in cultivation. Plants have cycles of popularity and disfavor.

The problem of keeping plants available as sources for species improvement is dealt with in various ways. Botanic gardens devoted to native plants exist throughout the world. City park systems sometimes include arboretum plantings of both native and foreign trees and shrubs. Certain large private estates in Europe and the United States also maintain outstanding plant collections. These sources are declining somewhat, however, as economic and population pressures make them more difficult to maintain.

Plant breeders are disturbed by a tendency toward destruction of potentially valuable gene sources. Plants that do not seem important now may become vital later on. In the more densely inhabited parts of the world, the gene bank of wild materials is being destroyed by dams, fire, and rapid urbanization, the inevitable results of the population explosion.

Many endemic shrubs that exist only in small restricted areas have a very precarious existence. For example, in California, on Santa Catalina Island where goats, wild pigs, and bison have been released, many unique species have been greatly reduced or destroyed. A recent botanical survey of the island failed to locate about 40 species that had been listed in a previous inventory. *Lavatera assurgentiflora*, an attractive, tall, ornamental flowering plant, sometimes used as a windbreak in vegetable growing, is now virtually extinct on the California Channel islands where it is native and grows only on a few offshore rocks. It conceivably could some day be lost to cultivation.

The introduction of the major ornamental shrubs from regions having a temperate climate is described by Coats (1963). Most of the ornamental shrubs have not been the subject of extensive cytological or genetic studies. Authentic information of this type prevents much wasted effort, particularly in attempts at interspecific hybridization. A detailed knowledge of the origin of garden forms is always valuable as there may be a need to reconstruct the horticultural forms from the original wild plants.

Some of our important ornamental plants have been developed slowly through the efforts of many people. Impressive advances have been made with plants of interest to hobbyists, through specialist societies, which usually include professional breeders, cytologists, and geneticists as well as many amateurs. These societies exchange much information, encourage collections, and facilitate the exchange of breeding material. They also stimulate interest in plant introduction, which is essential for real progress in the breeding of plant types that include many available species or geographic races.

Sources of variability in wildland shrubs

This paper reviews the sources of variability in shrubs and suggests some aims for improvement programs. In any program of plant development, we need to obtain as much variability as possible and then select the most desirable forms. Often there is much more variability in open-pollinated populations of a given plant than might be expected. Again, where interspecific hybridization is possible, the range of variability can be greatly extended.

Regional variation

The creosote bush, *Larrea divaricata*, is an attractive ornamental useful in several of the desert areas of the American Southwest. Yang (1967a, 1967b, 1968) has found considerable regional variation in this species. Compared with the Chihuahuan desert type, the Sonoran desert type is less tolerant of cold but is more drought resistant. The Sonoran desert form is taller and more erect and also more open in growth. The germination rate and the initial growth of the seedling were found to be slower. Yang and Lowe (1968) found that the chromosome number of the Sonoran form was 2n = 52 but for the eastern form in the Chihuahuan desert it was 2n = 26. The Sonoran desert has lower rainfall and higher winter temperatures than the Chihuahuan desert. Obviously, in ornamental plantings it would be advisable to use the local adapted forms. Yang (1968) also found a form from the Mohave desert that was very vigorous and variable and contained hexaploids. Leaf forms of each of these geographical races were distinctive.

Another desert plant that varies considerably when grown from seed is the desert holly, *Atriplex hymenelytra*. Found in the low-elevation deserts of the Southwest, it has an attractive silvery foliage sometimes collected for use in floral arrangements. Considerable variation may be observed in size, shape, and substance of leaves. One type has small leaves with little substance, but another has large leaves with a heavy leathery texture. It is difficult to grow under garden culture, but commercial plantings have apparently been made in the desert. The desert willow, *Chilopsis linearis*, has considerable flower variation, and horticultural forms have been selected. Roof (1966) reported that *Rhamnus californica* is a very variable species with low forms; one type has bluish leaves.

Physiological characteristics of a species may vary greatly among plants collected from different latitudes of the species range. Thus, Smithberg and Johnson (1967) collected plants of red-osier dogwood from various locations in the United States, Canada, and Mexico. Those from the northern regions produced winter buds, turned red, and dropped their leaves much sooner than those from further south. Fuchigami, Evert, and Weiser (1971) compared a red-osier dogwood from Dickinson, North Dakota, and from Seattle, Washington. The North Dakota form became acclimated to cold as much as 8 weeks earlier than the form from Seattle. However, there was little difference in the basic cold hardiness of the two forms.

Carpenteria californica is an attractive endemic plant found only in a few places in the Sierra foothills near Fresno, California. Such a plant might be expected to have little or no variation, but garden plantings show great differences in the size of the flowers. The more desirable forms with larger flowers are therefore propagated from selected seedlings by greenwood cuttings.

The shrub *Pittosporum tobira* varies greatly in compactness of growth when grown from seed. According to Leiser (1968), it illustrates introduction of a plant from one particular geographic locality, suggesting that further exploration and introduction of other forms, particularly from colder locations, which could be expected to produce more hardy forms, would be justified. Other plants vary greatly in character of growth when produced from seed from different localities. Leiser has also shown how the traditional idea of a well-defined stable species has tended to limit plant introduction and breeding until recently. He stresses the need for a much broader basis for plant introductions. Unquestionably, some species should be reintroduced.

Mutation

Valuable plants have been discovered by watching for mutations. Regel's privet, *Ligustrum obtusifolium regelianum*, was a sport that appeared about 1885. Menzies (1967) reported that a chance seedling from *Leptospermum scoparium keatleyi* produced large single cardinal red flowers. *Ilex cornuta burfordii*, a chance variation picked up in a Southern nursery, has practically replaced the original form of this species in the nursery trade.

Artificial induction of mutations, such as ionizing radiation, has not been very much used in shrub breeding. There are indications that colchicine treatment to induce increase in chromosome number is potentially useful. Sax (1947) treated a seedling of *Forsythia intermedia* with colchicine, and produced a tetraploid with erect stems, thick leaves, and larger flowers with darker color. This plant was also hardier than most of the species.

Objectives of a breeding program

Plant breeding has become a sophisticated technology using modern methods. We may expect more rapid progress now that professional, well-trained plant breeders are beginning to work with woody ornamental plants. Objectives for a program of improvement of woody plants may center on plant habit, foliage, flower and fruit characters, disease and insect resistance, tolerance of cold and heat, or ease of propagation.

Special forms

The habit of shrubs is important. Some forms of forsythia are gracefully arching and may be preferred over stiffer and more formal types. Compact slow-growing forms of shrubs are always welcome. They require much less pruning in the garden, and are also adapted to clipping to form plants of a formal character. A compact form of a useful seashore shrub, *Myoporum laetum*, has recently been introduced by the Los Angeles State and County Arboretum. A recent nursery introduction is a dense, compact form of Carolina cherry, "Brite 'n Tight," which has deep evergreen foliage and a well-branched upright form. There is a compact form of *Nandina domestica*, the heavenly bamboo, and dwarf forms of numerous standard landscape plants. Seedlings from a semidwarf form of the Australian brush cherry, *Syzygium paniculatum*, grown at the University of California, Los Angeles, produced a number of very dwarf types that may be introduced. Dwarf forms of many species of conifers are available. In recent years, some low-growing bougainvilleas such as the variety "Temple Fire" have been propagated and sold as ground covers. As a general rule, dwarf forms of almost any plant are welcome and used in landscaping.

Foliage color and texture are also valued in ornamental shrubs. A deep, rich green color is widely useful in landscaping, and glossy qualities are often prized. Of the various types of the Japanese privet, the form most frequently seen is the cultivar "Texanum," with unusually thick, deep green leaves. Other shrubs, such as the Australian brush cherry, are valued for the reddish color of their foliage. Many shrubs have cultivars with white leaf variegations, such as *Rhamnus alaternus* or *Pittosporum tobira*. Others have various types of yellow variegation such as *Aucuba japonica picturata* or "Sulfur." The "Vicary Golden" privet is an example of a yellow-foliaged plant. Interesting white and yellow leaf variegations occur in hollies. Japanese maples are available in many cut-leaved or colored-leaved forms that are propagated by vegetative means. The purple-leaved plums are derived from various species and are commonly used in landscaping.

Flower production

Many shrubs are prized for their flowers. Some, such as the camellia, *Leptospermum scoparium*, and the gardenia are commercial cut flowers. Azaleas and other flowering or fruiting shrubs are grown as pot plants. A wider color range is always desirable. In camellia breeding today, the elusive lavender or blue tones and yellow are sought. Sometimes hybridization is the answer. Thus, a few years ago the only available species of trailing lantana had a lavender color. Howard (1970) has described interspecific hybridization of the bush lantana, *Lantana camara*, which has given spreading or trailing types in many of the bright colors of the bush lantana with the habit of *L. montevidensis*. A hybrid of *Berberis amplectans* and *B. aquifolium*, "Golden Abundance," has much showier flowers than either parent species.

Interspecific hybridization

Substance and keeping quality of flowers are both important. In recent years in California, interspecific hybridization has produced a new race of Chinese hibiscus which keeps flowers open for several days instead of only one--obviously a valuable contribution. The commercial cultivars of roses show great difference in the lasting qualities. Recently florists have introduced some new forms of poinsettias that have truly remarkable lasting quality; the Paul Mikkelsen variety is an example.

Extending the season of bloom is a desirable aim in improvement of flowering shrubs. Thus, more good early varieties of *Camellia japonica* are needed. Interspecific hybridization has extended the blooming season of lilacs.

Flower size, fragrance, and double form are all valued characteristics. The emphasis is usually on larger flowers, but there is some breeding for miniatures, which have their own special charm. The camellia is presently being hybridized with several of the fragrant species. Much rose breeding in recent years has tended to reduce fragrance, but fragrance is always desirable. Double flowers, formed by transformations of the stamens into petals, are often prized for garden cultivation. They are usually uncommon in the wild since they set fewer seeds and have a negative survival value.

Decorative fruits

Fruits are the chief ornamental feature of some shrubs, such as pyracanthas or cotoneasters. Fruits vary in color and size and in the way in which they are borne. Thus, some pyracanthas produce berries evenly along the stems, but others produce them in large separate masses. The fruits of other shrubs such as barberries have brilliant colors and are carried well into the winter, a valuable feature for cold climates. Fruits of some selections of shrubs appear to be less attractive than others to birds. The fruits of toyon from a California Channel island form that does not breed true from seed are much larger than those of the mainland form. The Channel Island toyon is

attractive and worth cultivating by vegetative means; a disadvantage is that the fruit is so heavy that the branches droop when used in arrangements. Some color phases of ornamental fruits are known, such as yellow-fruited holly and yellow-fruited toyon.

Resistance to disease and harsh climate

Resistance to disease and hardiness to cold weather may be the aims of improvement programs. Fortunately, most ornamental shrubs do not have serious diseases, but a few, such as the petal blights of azaleas and camellias, have been introduced and have spread in recent years. Fire blight is sometimes troublesome on pyracanthas. *Pyracantha angustifolia* is susceptible, but most of the other species have some resistance. A blight-resistant form of *Juniperus sabina tamariscifolia* is now available. Plants differ in their susceptibility to insect attack.

Creech (1966) listed several ornamentals especially suitable for cold regions that were found in 1934 by an expedition sent to the Balkan States by Arnold Arboretum. A collection of privet from near Sarajevo, Yugoslavia, was tested in Wyoming and South Dakota and found to be unusually hardy, surpassing even the Amur River North privet. The Yugoslavian privet was introduced in 1965 under the cultivar name "Cheyenne." A hardy boxwood, "Vardar Valley," was deliberately collected by this expedition at a cold site.

We know now that plant introduction offers the chance of replacing present cultivars with hardier forms. Hybridization of tender and hardy forms often combines the desirable horticultural characteristics of the tender forms with the cold resistance of the hardy forms. The "Glenn Dale" azaleas of Morrison (1953) were produced in this way.

Breeding for greater hardiness is applicable to various climates. In such subtropical regions as Florida and California, frost often damages subtropical plants in less favored sites. In the north-central United States, few broad-leaved evergreen trees or shrubs are available; consequently, the hardy forms of pyracantha, holly, and Korean boxwood are of great interest. On the other hand, some fruit and ornamental plants do not get sufficient chilling in the average winter in southern coastal California or in Florida to break winter dormancy. Many varieties of lilacs and peaches are typical. There has been some breeding of lilac forms that will break dormancy easily. Some of the early blooming forms require less chilling and have been used in breeding. *Syringa persica laciniata* is also used. These shrubs have not excited great interest thus far, possibly because they are deciduous.

Ease of rooting of cuttings is sometimes considered in selection of plants. *Raphiolepis* hybrids often vary in this character, and the clones selected for introduction are chosen for this quality as well as for plant habit and flower characteristics.

Sometimes one sex of a plant is more desirable horticulturally than the other. The preferred male form of the prostrate coyote bush, *Baccharis pilularis*, a drought-resistant ground cover much used in recent years, does not produce the undesirable white pappus.

The Rancho Santa Ana Botanic Garden has produced from material collected at Twin Peaks near San Francisco two cultivars having desirable horticultural qualities, "Twin Peaks No. 1" and "Twin Peaks No. 2." The latter is slower growing, has larger leaves, and is probably the better. On a slope these forms do not need clipping. These illustrate the improvement to be obtained by selection of wild forms without hybridization.

Shrub improvement by breeding

Recent activity in shrub breeding is illustrated by progress with ceanothus, fuchsias, and camellias, which have been improved through interspecific hybridization.

Ceanothus

Ceanothus, a group of wild plants of the Western Chapparal zone, seems to offer considerable opportunity for additional breeding. According to the monograph by Van Rensselaer and McMinn (1942), California has 45 of the 55 species, 22 of the 25 varieties, and all 11 of the natural hybrids. Five species grow east of the Mississippi River, and a few grow in Mexico. The group includes forms ranging from low trees through average-size shrubs to small prostrate forms. They are found from the seashore to high mountain areas. Most types are somewhat drought resistant, but unfortunately some types are susceptible to root rots and are short-lived when grown under garden conditions with ample watering. In recent years, several new species, often with horticultural value, have been discovered. One of these, *Ceanothus cyaneus*, a rich blue species in San Diego County, is difficult to grow in gardens, but has been valuable for hybridizing; it is a parent of the useful garden varieties "Sierra Blue" and "Mountain Haze." Other newer species in cultivation are *C. roweanus*, *C. sonomensis* and *C. mansonii*. Other valuable forms may yet be discovered. Many ceanothus species hybridize freely when grown in proximity. Seed of such types should be saved only from isolated natural stands.

Two prostrate forms much used in gardening are *Ceanothus gloriosus*, the Point Reyes creeper, and *C. griseus horizontalis*, the Carmel creeper. Another popular garden form is *C. impressus*, the Santa Barbara ceanothus. Derivatives of this species, such as "Concha," appear to stand garden watering particularly well.

Some ceanothus apparently have special climatic requirements and are not cultivated successfully out of their native range. Under cultivation, certain types tend to be somewhat short lived, but some of the new hybrids appear to be better suited to cultivation than some of their parents.

Fuchsia

Fuchsia is unusual in shrub breeding in that its parentage is known to be complex. The foundations of fuchsia breeding were laid early in the nineteenth century in Europe, especially in France, Belgium, and England. Unfortunately, the parentages of most of the important foundation varieties are unknown because they were kept as trade secrets by the originator. Some varieties are apparently hybrids between various forms of *Fuchsia magellanica* and *F. fulgens*. Some characters appear to be derived from *F. boliviana* and *F. cordifolia*. Species that also entered into early hybrids were *F. corymnbifolia, F. formosa elegans, F. globosa, F. corallina,* and *F. coccinea.*

Certain mutations were soon used in breeding. The appearance of the white corolla finally has terminated in practically all white varieties. Doubling of flower parts has been popular and is now represented by many different varieties. An interesting marbling of color has also appeared but is somewhat unstable. Several types of growth habit are useful for specific purposes. Considerable breeding is being done in California, based mostly on the European strains. Some breeders have selected strains that tolerate more than the usual amount of heat and low humidity. Reiter (1944, 1945) recorded the known history of fuchsia breeding. Unfortunately, little is known about the inheritance of color in this group, but white flower color is known to be recessive. Doubtless the fuchsia has possibilities for future breeding; some species have not yet been used for development.

Camellia

The unusual amount of breeding activity in the camellia group might be a pattern for other groups. More than a century ago, the camellia had a great vogue both in America and in Europe. It was much planted in the States of the American South. Unfortunately, the Civil War destroyed much of the wealth and culture of that region, but many magnificent specimens of camellia remained on the old plantations. Names of many varieties were lost during that period, and considerable research in recent years has been directed toward establishing their identity. The breeding activity in the pre-Civil War period was largely confined to production of varieties of *Camellia japonica.*

Interest in these spectacular landscape shrubs has revived. Many local and national societies devoted to study and propagation of this flower have been organized. Their exhibitions emphasize the display of cut flowers of highest quality and largest size. The excellent landscaping qualities of *Camellia sasanqua* were recognized, and many varieties became available. Some were surprisingly resistant to cold, and the limits of culture moved northward. Parks and Armstrong (1971) have described breeding and selection programs having this objective.

Interest accelerated after World War II. The remarkable interspecific hybrids made by the late J. C. Williams at Caerhays Castle in Cornwall have exceptional landscape value. These were hybrids of *Camellia saluenensis* with *C. japonica*; they have been described by Shuey (1971) and are still designated as Williamsii hybrids. *Camellia cuspidata* has been introduced into this group.

The camellias most remarkable for size of flower are the various forms of *Camellia reticulata* that have been introduced recently. Previously a sterile form, "Captain Rawes," was known in cultivation. These new forms are being found to be fertile with other species. Hybrids with *Camellia sasanqua* are being introduced into the nursery trade and are prized for their very large flowers. Savige (1971) reported that hybrids with *C. pitardii* var. *yunnanensis* produced fine foliage and light flowers. *C. reticulata* is very tender, but some hybrids have resistance to cold. *C. reticulata* has also been crossed with *C. saluenensis*. Craig (1971a, 1971b) has described the Higo camellias of Japan, which are hybrids of *C. rusticana* and *C. japonica*. Another new and promising species is *C. granthamiana.*

Cutter (1971) has described breeding for fragrance using the species *C. lutchuensis* and *C. fraterna*. Other species have an unpleasant odor.

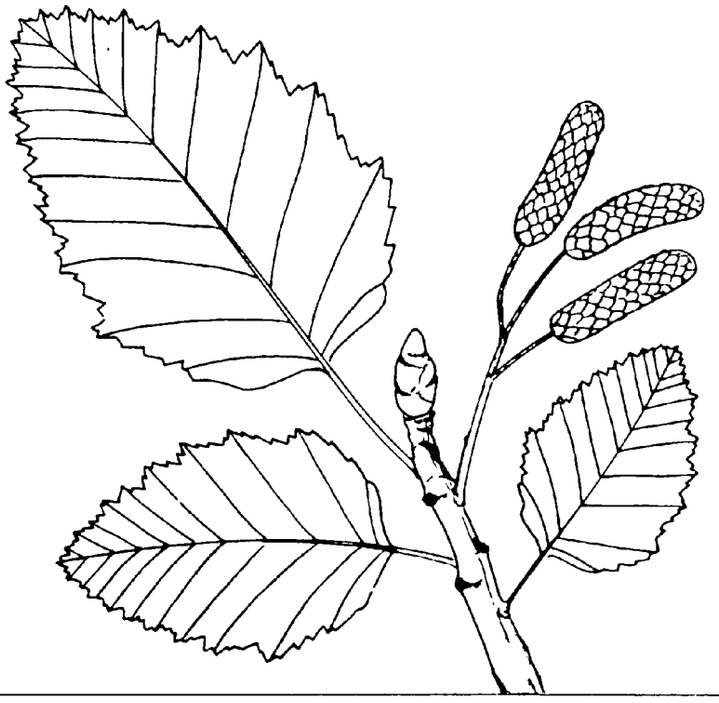
Hilsman (1966) and Parks (1968) have listed various interspecific hybrids of camellia. Ackerman (1970) tried 206 interspecific combinations of 21 species; many were successful. More than two species have been combined. Camellias of the future will doubtless have complicated pedigrees, but fortunately, present-day breeders are keeping careful records.

Aside from the great interest in interspecific hybridization of camellias, some attention is being given to the inheritance of flower colors. If China should again be open to exploration, a new impetus to introduction and breeding would undoubtedly follow; but the possibilities of the material already at hand are being exploited fully.

These illustrate the rich possibilities for improvement of shrubs that have a wide geographical range. Many shrubs meet this requirement in both subtropical and colder regions. Application of modern plant breeding methods to shrubs should give us many new plants in the future.

Section IV.

Synecology



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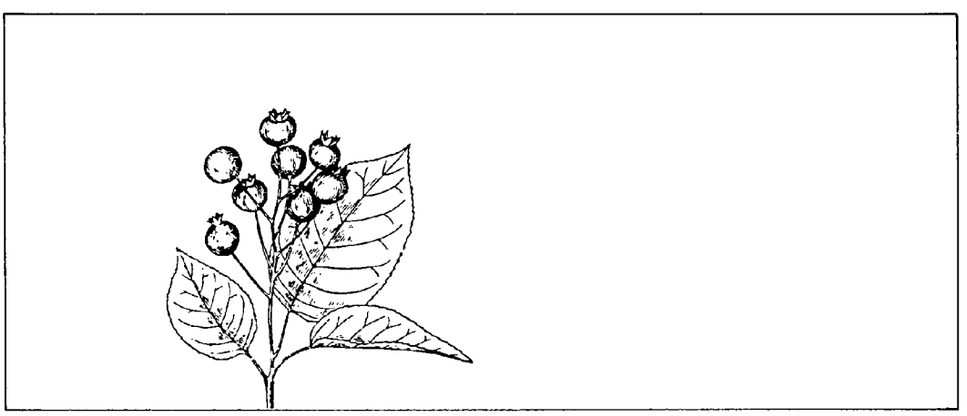

Salt desert shrub response to grazing use

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As early as 1902, Griffiths pointed to the deterioration of salt desert shrub ranges. Speaking of *Eurotia lanata* (Pursh) Moq., a useful feed for both cattle and sheep, he said ". . . it is very much injured by overgrazing. . .. To say that the southern portion [of Nevada] is overstocked, would be putting the matter very mildly." Throughout the years, the deterioration of North American salt desert shrub communities under grazing and the ecological replacement of choice forage species have been described repeatedly (Wooton 1932; U.S. Forest Service 1936; Stewart and others 1940; Barnes 1926; Shantz and Piemeisel 1940).

The first signs of deterioration of salt desert shrub range are reductions in size, vigor, and number of desirable forage plants in the cover. Concurrently, soil stability decreases. Annual weeds and grasses become abundant in years favorable for their growth and in time, less desirable species (shrubs and herbs) increase and attain dominance.

Similar ecological changes have resulted from grazing the arid and semiarid regions of Australia, according to Wood (1936) and Ratcliffe (1936). Knowles and Condon (1951), writing of the Hay Plain of New South Wales state that "the most important plant from the graziers' point of view is the perennial saltbush" (*Atriplex vesicaria*), which they assumed to have existed "in thick stands over the whole of these areas" before settlement by Europeans. "Today, due to overgrazing and, to some extent, drought, good stands of perennial saltbush are a comparative rarity..." These and other Australian observations (Osborn, Wood, and Paltridge 1932) are reminiscent of reports already cited describing conditions in Western United States.

A unique range type

As livestock range, the salt desert shrub is unique among American grazing lands. Due to the arid climate (precipitation, 4 to 8 inches (10 to 20 cm.) annually), herbage yields and carrying capacities are low. About 1-1/2 to 3 acres (0.6 to 1.2 ha.) are needed to support a sheep for a month; about 10 to 20 acres (4 to 8 ha.) or more are needed for a cow.

The salt desert shrub is primarily a browse range, and shrubs or half-shrubs provide most of the feed for livestock, particularly sheep. Among the several range types listed by Costello (1944, table 26), the salt desert shrub range is the only one on which more than half the forage resource (65 to 90 percent) is browse. Even on mountain types designated as brush areas, most of the forage is herbaceous.

In the main, the salt desert is a winter range. It serves as a "holding area" for maintenance of breeding or gestating livestock; so nutritional requirements are relatively low. Nevertheless, the living twigs of dormant browse plants, some with persistent seeds, make this range type more nearly adequate for animal maintenance (Cook and others 1954) than other cold-weather ranges where the aerial plant parts are dead.

In world grassland (i.e., grazing land) literature, shrubs are generally considered a curse, except as wildlife habitat. Unlike grass ranges, where deterioration often results in encroachment by unwanted shrubs, the salt desert shrub is a range on which management hopes to perpetuate woody and suffrutescent species.

Description of the North American salt desert

The salt desert shrub range in the cold desert and steppe climates of North America is a mosaic of many communities in the plains, foothills, and valley edges of the Great Basin and in the northern part of the Colorado Plateau. Outliers are found in some arid valleys of the Rocky Mountains and eastward on parts of the Great Plains (fig. 1). Low shrubs or half-shrubs dominate the aspect. In some areas, perennial grasses share dominance with the low shrubs in a yield ratio of about 1:4. Usually only 5 to 15 percent of the ground surface is shaded by living plant cover. The mosaic of plant communities is composed of homogeneous units ranging from less than an acre to thousands of acres in size. The pattern is a function of variations in soil characteristics.

The growing season begins as early as the first of March for some species and 2 or more months later for the warm-season plants. Killing frosts occur in October and November, but the number of growing days in the growing season depends less on temperature than on soil moisture, which is variable and erratic.

Superimposed on the mosaic as the principal biotic factor is the domestic grazing animal. Many of the native salt desert plants are palatable and nutritious, and the deserts are used primarily for winter grazing. On approximately 40 million acres (fig. 1), we winter about 3 million sheep and hundreds of thousands of cattle each year.

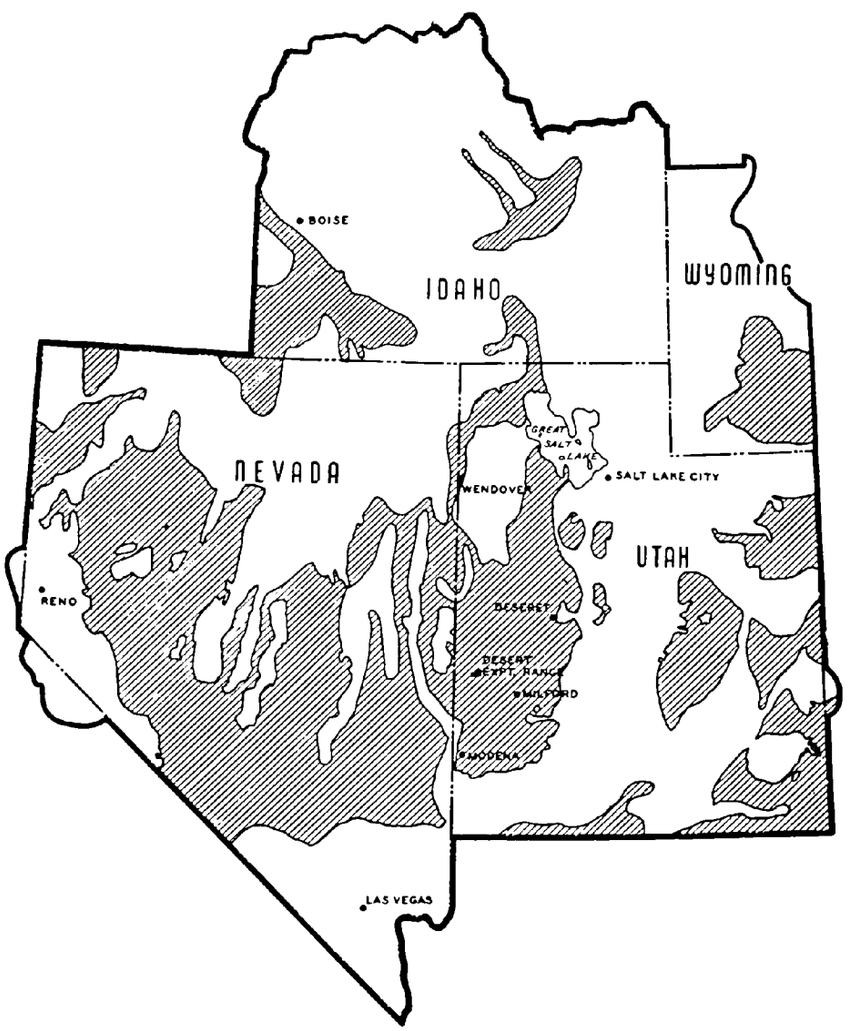

Figure 1.--Winter range area (shaded) in the Intermountain States. Most of this is in the salt desert shrub zone. (From Hutchings and Stewart 1953.)

Important plant species

In general, the browse species are sufficiently high in protein to satisfy the animals' nutritional requirements, but they are low in energy values. A few (notably the *Artemisias*) contain near-adequate amounts of phosphorus. Grasses, on the other hand, have sufficient digestible energy, but are low in protein and phosphorus (Cook and others 1954). Over most of the desert area, both shrubs and grasses are found in direct association or in adjacent communities, so a suitable diet is available for the livestock.

Palatability would seem to be the character most important for ranking the species as to desirability. Also important are dependability of production and a growth form that permits a considerable proportion of the production to be utilized.

Throughout the winter, *Artemisia nova* A. Nels. is nutritious and consistently palatable to sheep. *A. spinescens* D.C. Eat., also nutritious, is generally palatable only in late winter, but some years it, too, is utilized all winter. Both of these sagebrushes are much more highly preferred by sheep than by cattle. *Eurotia lanata* is used by both sheep and cattle. It varies somewhat from year to year in palatability and, consequently, in degree of use. *Eurotia* is nutritious, but it is not as high in phosphorus as the *Artemisias* (Cook and others 1954). *A. nova*, *A. spinescens*, and *E. lanata* are considered "desirable" browse species.

Atriplex confertifolia (Torr. & Frem.) Wats. is palatable, and the persistence of its seeds on the pistillate plant through the winter enhances its nutritional value. Its twigs become sharp dry spines at maturity, so only the leaves and seeds are eaten in winter; the spiny habit prevents utilization of more than 15 to 20 percent of the previous summer's total herbage growth. For this reason, we do not consider it desirable where other species would yield larger harvestable proportions. It is not injured by winter grazing; instead, it increases in abundance under heavy use in several of the salt desert types. However, on severely overstocked range, even this species can be damaged.

Chrysothamnus stenophyllus (Gray) Greene is an undesirable plant because of its generally low palatability. It, too, increases on overgrazed ranges.

The cool-season grasses, *Oryzopsis hymenoides* (R. & S.) Ricker, *Sitanion hystrix* (Nutt.) J. G. Smith, and *Poa sandbergii* Vasey, are sometimes green from autumn rains when freezing weather comes. They begin growth again in early spring while the animals are still on the winter range. These species are highly palatable and are the most desirable of the desert grasses.

The warm-season grasses are more variable than most other species in amount of annual herbage production; yield varies with the amount of summer precipitation. Palatability during the season of winter dormancy also seems to be more variable for the warm-season grasses than for the cool-season grasses. As a group, the warm-season grasses are less desirable. Winter use does not injure them; in fact, some of them increase under heavy grazing. Important among the warm-season grasses are *Hilaria jamesii* (Torr.) Benth., *Sporobolus cryptandrus* (Torr.) Gray, and *Bouteloua gracilis* (HBK.) Lag.

A number of annuals grow in association with the shrubs and grasses of the salt desert. Ordinarily, they are rare, generally being confined to sites of recent disturbance. On overgrazed range they are much more common. The specific kind of annual present, its density, and its yield are extremely variable from year to year and from place to place. In some years, there are few if any annuals, even where perennial competition is lacking.

Native annuals seldom comprise more than a small fraction of total cover. But three old-world species produce abundantly on poor condition range when the amount and time of precipitation are favorable. These are *Bromus tectorum* L., a winter annual, and *Salsola ali* L. and *Halogeton glomeratus* (Bieb.) Meyer, two chenopodiacious summer annuals. *Halogeton* is undesirable because it is poisonous. The other two are both palatable and nutritious, but being annuals they are an undependable feed source.

Goals of range management

Because the North American salt desert is a range type that ordinarily receives only light snowfall, produces unusually high-quality winter forage, and is in juxtaposition with other ranges unsuited for winter grazing, its highest and most valuable use is winter range for livestock. Such use is not incompatible with its present and potential value for wildlife habitat and recreational activity. Due to its vast expanse and its high altitude (4,000 to 7,000 ft.), there is little likelihood that even comprehensive long-range plans for water importation would change this prescription for most of the salt desert shrub area.

As is the case with ranges the world over, this range deteriorates under unwise or abusive use and much of it is already in a depleted state. Consequently, the goal of range managers must be to maintain the ranges still in good condition or to improve ranges that have deteriorated.

The grazing land we call the "winter range" is in fact a winter-spring range. Most bands of sheep use the salt desert shrub areas from November through April. Cattle are there, usually on separate range units, for the same period, and on parts of this range type, cattle graze at other seasons of the year as well. Because of our terminology, we tend to think of the forage harvest as dormant-season grazing, but many salt desert plants begin to grow 1, 2, or more months before the grazing season ends. As we note later, spring is the critical grazing period on this arid range type. Grazing at this season is detrimental to the plants because of the undependability of sufficient soil moisture for plant growth and recovery after being grazed.

Demand is high for ranges to graze in spring, and few other areas are available for grazing at that time; so the salt desert must do a double duty over much of its area. How to provide both winter and spring forage for the animals this range must accommodate is one of management's primary problems.

Again, the amount of grazing that desirable plants can endure at any season and still remain vigorous and productive is limited. A range manager must know the limit, but thus far, research has provided only a part of the information he needs. We have acquired some information on potential site productivity, a concept of natural vegetation, its structure and composition. We have followed some of the processes of plant succession in the directions both of improvement and deterioration. We have learned that salt-desert ranges can improve under grazing, and we know that the economic benefits more than offset the costs of improved management practices (Hutchings and Stewart 1953; Hutchings 1954).

But the salt desert shrub vegetation is composed of a variety of communities and results of studies at one place may not be widely extrapolable. Thus far, the physiological aspects of the effects of grazing on plants have received only superficial attention and the ecological aspects have received little more; only the most direct sheep-plant relations have been looked into. Nevertheless, results of grazing and clipping studies in a number of places in the salt desert shrub range are in agreement (Hutchings and Stewart 1953; Fisser 1966; Turner 1971; Eckert 1954; Cook 1971), and certain general principles of management for this type are now apparent.

Successional change

Experimental work on salt desert shrub ranges in North America was started by the Forest Service in 1931. During the 1930's a large number of 4-acre (1.6-ha.) exclosures were constructed in Utah and Nevada to exclude livestock and to permit observations of successional changes on both grazed and ungrazed range. In 1933, the Desert Experimental Range was established by the Forest Service in a salt desert shrub type in western Utah. The examples of vegetational response to grazing treatments presented here are from these studies.

Scientists in universities and other agencies and institutions have reported results similar to ours for other sites in the Western United States (Eckert 1954; Cook and Hurst 1962; Cook and Stoddart 1963; Marquiss and Lang 1959; Fisser 1966; Cook 1971). On Australia's halophyte ranges, where grazing seasons and annual temperature regimes are quite different from those of the North American salt desert shrub, vegetation has responded to various grazing treatments in much the same way as it has in America (Osborn and others 1932; Barker and Lange 1969).

At the Desert Experimental Range, 20 pastures, either 240 or 320 acres (97 or 130 ha.) in area, have been grazed by sheep, each at one of three intensities (heavy, medium, or light) and for one or more of three seasons (early winter--November-December; mid-winter--January-February; or late winter--March-April) for 36 years. In general, light and medium grazing intensities have shown essentially similar effects; heavy grazing has resulted in a different plant response. The two seasons of plant dormancy had much the same effect on plant cover; the season of early spring growth (late winter) differed from them in its effect. For practical purposes then, we can consider our grazing treatments to have been two intensities (moderate-or-lighter and heavy) and two seasons (dormancy and that of early spring growth).

Several large range units varying in area from about 1,300 to 5,800 acres (525 to 2,350 ha.) are in the neighborhood of the pastures.[1] These units are grazed at different periods of the winter. Each treatment has been applied to its assigned unit since 1935. There are also some ungrazed areas (exclosures) on the experimental range.

Grazed and not grazed

Let us compare the change in shrub cover under winterlong (November-April) grazing with that on areas not grazed. The Snake Valley area is a potential *Artemisia nova* community and no doubt supported *A. nova* before it became a sheep range about 70 years ago. The composition values for 1937 (table 1) express the influence of decades of heavy winterlong use prior to the start of this study. *Atriplex*, as we have already noted, increases as the more desirable species are weakened, and we assume that this happened at Snake Valley. In 1937, *Eurotia*, a species more useful than the *Atriplex* and less palatable than the *Artemisia*, was a codominant with *Atriplex*. As the original treatment was continued, *Eurotia*, too, gave way to *Atriplex*, which by 1947 was the only major shrub on the grazed area.

In 1961, this area became a winter range for cattle, and by 1964, a different trend of compositional change was apparent on the grazed area. The direction of change was reversed for two species; some *Atriplex* plants died or showed a reduction in vigor, and the previously low-vigor *Artemisia* plants increased in size. *A. nova* is not relished by cows to the extent that it is by sheep; so its response to the change in livestock was similar to what had happened several years earlier under total protection from grazing. On the other hand, *Eurotia* continues to be grazed by the cows, as it previously

[1]Maps on p. 5 and 6, Hutchings and Stewart (1953), show treatments for pastures and grazing units.

Table 1.--*Percent composition (derived from weights) of the shrub component at Snake Valley*

Shrubs	Grazed			Not grazed		
	1937	1947	1964	1937	1947	1964
Artemisia nova	6	6	25	5	36	63
Eurotia lanata	42	8	10	44	12	8
Atriplex confertifolia	50	80	58	47	44	22
Other shrubs	2	6	7	4	8	7

was by the sheep; so it is at more of a competitive disadvantage now than it was earlier. On the ungrazed area, *Eurotia* could not compete with the *Artemisia* and so was almost completely replaced by it. It is probably safe to predict that, under future winter-spring grazing by cattle, this Snake Valley site will eventually become a predominantly *A. nova* community similar in composition to the ungrazed area.

Table 1 ignores herbaceous species, but in 1937, perennial grasses comprised about 20 percent of the vegetation by weight). They are still abundant on the grazed area, but on the ungrazed area, competition with *Artemisia* has materially reduced grass yield. Under grazing by cattle, grass is at a double disadvantage and is expected to decline.

If our predictions are correct, the cover will revert to the original *A. nova* community. If it does, it will be a case of secondary succession under grazing to a type much the same as the pristine. But, as a cattle range, its forage productivity will become less as *Artemisia* becomes dominant.

Figure 2 shows another comparison of grazed and ungrazed *Artemisia nova* sheep range. Under grazing pressure, the undesirable species that increases on this Newark Valley range is *Chrysothamnus stenophyllus* instead of *Atriplex*. However, the relation of *A. nova* to grass and *Eurotia*, and to the undesirable shrub is much the same here as at Snake Valley. The fact that the undesirable shrubs are not the same under grazing disturbance at the two sites is attributable to soil differences.

The retrogression of the *Artemisia* type under heavy continuous grazing pressure to a variety of subseral conditions is an example of site differences within an apparently homogeneous plant community becoming obvious under deterioration. On the other hand, there can be a positive change from a given disturbance community under protection to a number of different successional communities depending on the sites. For example, the *Atriplex-Eurotia* type at Snake Valley progressed toward *Artemisia nova* dominance. In other places, however, this type has become an almost pure *Eurotia* or a *Eurotia lanata-Artemisia spinescens* type under protection. And, a disturbance community of pure or nearly pure *Eurotia* may be succeeded under protection by *E. lanata-A. spinescens* or by *A. nova*, or it may remain predominantly *Eurotia*. The foregoing illustrates a problem about which we still have almost no understanding: the plant-soil relations of the salt desert shrub (Mitchell and others 1966; Gates and others 1956). More information is needed before we can confidently extrapolate results of our grazing treatments and make more sound recommendations for range management decisions.

At Pine Valley (table 2), *Eurotia* is the only important shrub. Although there has been ample opportunity for propagules of *Atriplex* and *Chrysothamnus* to reach this site, neither of these undesirable shrubs has become established, even under extremely heavy winter use that in some years has extended into late spring. Relative amounts of grass and *Eurotia* in the perennial cover have fluctuated somewhat on the grazed area, but the long-term trend has been an increase in grass. It now constitutes the greater part of

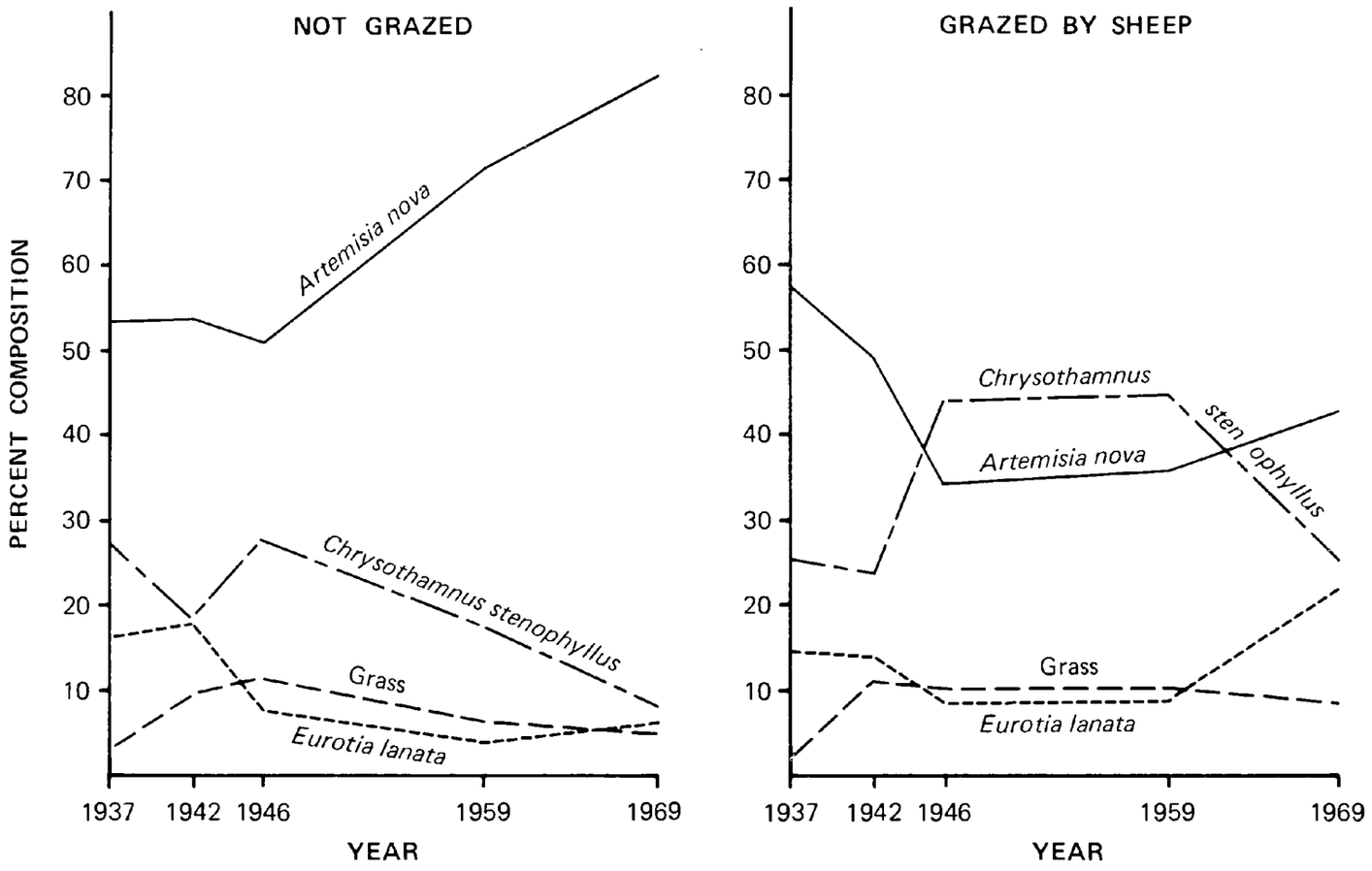

Figure 2.--Proportional amounts of perennial species under two conditions of grazing. (Newark Valley, Nevada.)

perennial plant productivity on the site. However, under protection, the relative amount of grass has steadily decreased. In fact, Pine Valley's tendency toward greater shrub dominance in ungrazed areas is similar to that of the Snake and Newark Valley sites and similar to most other (about 60) long-protected sites with which we are familiar on winter ranges of the salt desert. Under overgrazing in the winter and spring, the trend toward grassland is a rather common occurrence in many communities of this association and is similar to the response on overgrazed saltbush ranges in the winter rainfall areas of Australia (Box and Perry 1971).

In years favorable for their growth, annual weeds dominate the grazed community at Pine Valley; the contrasting absence of annuals on the ungrazed area is very pronounced. Suppression of annuals by ungrazed perennials has been the almost universal experience in grazing-exclosure studies. Turner (1971) has most recently shown this for another salt desert type.

Annuals on other than small areas of disturbance should be considered indicators of overgrazing or other abusive range use. Under moderate use, annuals are almost non-existent (Hutchings and Stewart 1953; Hutchings 1954; Fisser 1966).

Table 2.--*Herbage production (lb./acre)*[1] *at Pine Valley where an area was protected by a fence in 1937*

Types	Grazed				Not grazed			
	1937	1940	1946	1963	1937	1940	1946	1963
				PERENNIALS				
Eurotia lanata	49	29	62	52	36	171	121	167
Grass	15	12	13	47	16	68	51	32
Total[2]	67	44	77	108	53	240	175	206
				ANNUALS				
Weeds	115	146	3	98	77	11	t[3]	2
Total production	182	190	80	206	130	251	175	208
Usable forage[4]	49	40	45	70	38	141	110	115

[1]Conversion factor for kg./ha. = 1.121.
[2]Values include negligible amounts of other species.
[3]Trace.
[4]Calculated from average utilization records on moderately grazed sheep range. The assumption for the right half of the table is that the enclosure could be grazed, which of course it was not.

Intensity of grazing

In the experimental pastures, where the total herbage production has averaged about 220 pounds per acre (246 kg./ha.) a rate of stocking of about 17 sheep-days per acre (42 days/ha.) was determined to be too heavy. At this rate, production of the desirable forage species declined. Stocking rates of 12 or fewer sheep-days per acre (30 sheep-days or fewer per hectare) allowed the vegetation to improve in forage quality and quantity. These results are discussed in some detail by Hutchings and Stewart (1953).

Before the experimental range was established 38 years ago, an almost pure stand of *Eurotia* grew on the fine sandy loam of a flat valley bottom that became part of Pastures 18 and 19. Both pastures are grazed by sheep in late winter, Pasture 18 at the heavy rate, Pasture 19 at the medium rate. After 28 years of treatment (in 1963), composition in Pasture 19 was much the same as at the start, but the cover in Pasture 18 had changed to a less productive forage type as shown here:[2]

	Pasture 19		*Pasture 18*	
	(Lb./acre)		*(Lb./acre)*	
Eurotia lanata	122	(137)	45	(50)
Atriplex confertifolia	16	(18)	71	(80)
Annuals	11	(12)	42	(47)
Total yield	149	(167)	158	(177)
Usable forage	71	(80)	43	(48)

[2]Values in kg./ha. shown in parentheses.

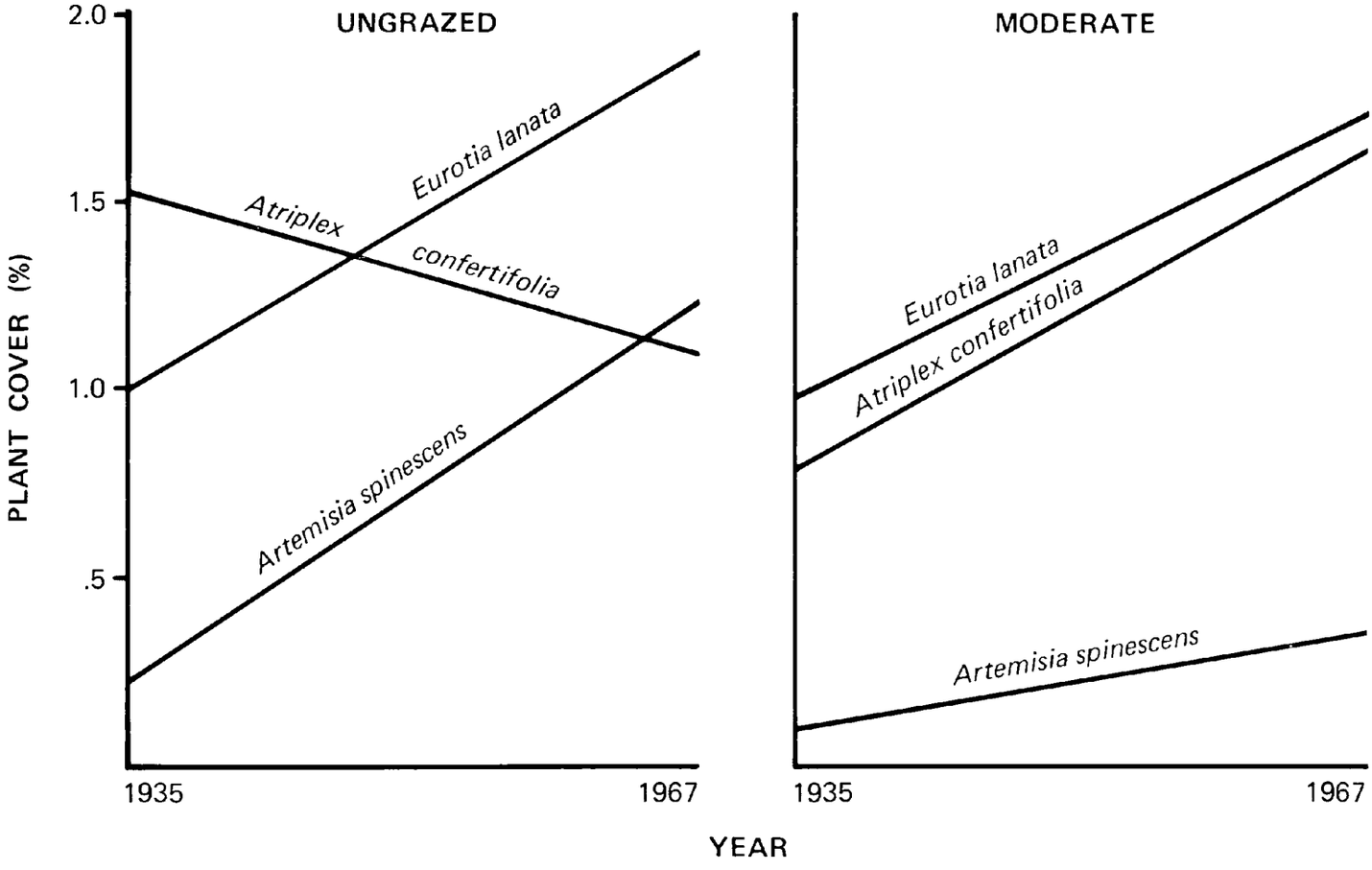

Figure 3.--Plant cover trends for species ungrazed (left) and for species grazed by sheep at a moderate intensity during winter (right). (Desert Exp. Range, Utah.)

Moderately grazed pastures can be compared with ungrazed exclosures located within them. The left half of figure 3 shows trend lines for cover by species in 10 exclosures, each 1 acre (0.4 ha.) in size, in five moderately grazed pastures. On the right, trend lines are given for the same species in ten 1-acre grazed areas in those pastures. The year 1967 was more productive of total cover than 1935; so the lines rise toward the right. The solitary exception is the trend line for *Atriplex*, which has definitely decreased on ungrazed areas. While *Artemisia spinescens* is replacing *Atriplex* on the ungrazed sites, a similar change is occurring at a much slower rate on grazed areas. *Artemisia* cover was more sparse at the start on grazed than on ungrazed areas. On the latter, *Artemisia* made a fivefold increase; under grazing, *Artemisia* cover increased 3-1/2 times. This relative change is greater than any other species increase shown on the right side of figure 3.

Season of grazing

The pastures grazed in late winter year after year have lost some of the most valuable plants for spring forage. The lines of figure 4 show trends of plant cover on heavily grazed pastures. Averages of values from pastures grazed in the first half of the dormant period are shown on the left side. The right side of the figure shows average trends for pastures grazed in late winter (actually after spring growth has started). Under early winter use (even at this heavy rate), forage quality is improving, although it should be remembered that *Artemisia spinescens* does not regularly contribute to the forage supply at this season. On pastures grazed heavily in late winter, *Atriplex confertifolia* has become dominant while the two most valuable shrub species have declined. One of them, *Artemisia spinescens*, has disappeared from these pastures. It has also disappeared from the less heavily used pastures that are grazed year after year in late winter (early spring).

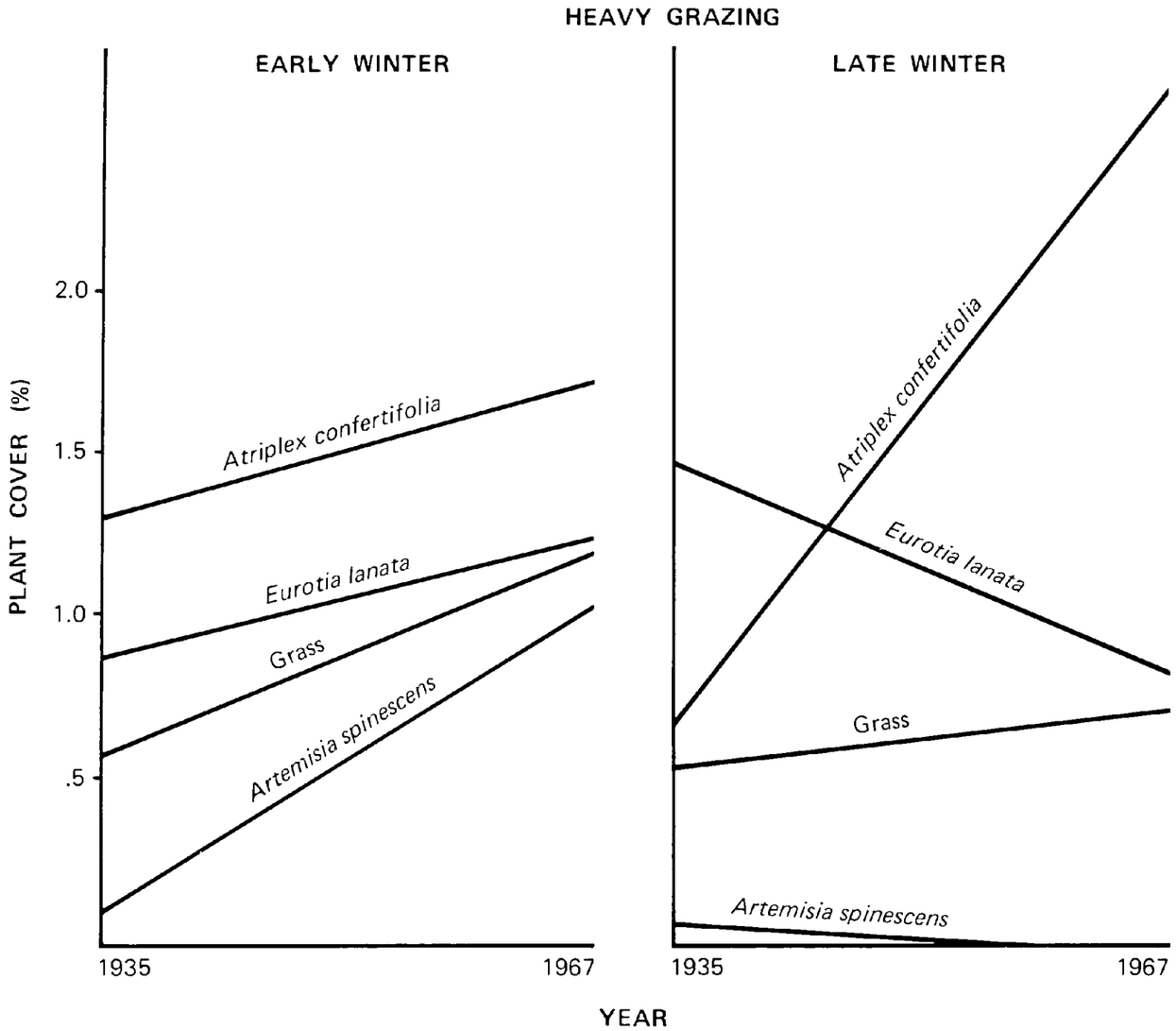

Figure 4.--Plant cover trends (regressions on time) for species grazed by sheep at a heavy rate of stocking. Trends at left are for areas grazed during dormant season; those at right are for areas grazed at the beginning of the spring growing season. (Desert Exp. Range, Utah.)

In the James neighborhood, on an *Artemisia nova-Eurotia lanata* site, *A. nova* had declined under decades of heavy grazing throughout the winter to a minor component of the cover by 1934. It has recovered remarkably under moderate early winter use since that date. Under continued winterlong use (also moderate in more recent years), no such recovery has occurred. Composition is poorer foragewise than it was in 1934 as shown in the following tabulation:[3]

	1934	*1963*	*1963*
		Early winter	*Winter-spring*
	(%)	*(%)*	*(%)*
Artemisia nova	7	54	8
Eurotia lanata	63	30	48
Chrysothamnus stenophyllus	23	13	42

[3]Percent of perennial vegetation; based on weights.

This site is similar to Newark Valley (fig. 2). Here, under early winter grazing, compositional change has proceeded in a direction similar to that on the ungrazed Newark site.

Season and intensity

An interesting comparison is found in Antelope Valley on an alluvial fan where *Artemisia nova* occurs in strips along the dry drainageways, occupying less than 10 percent of the total area. It is the most palatable of the species on this range and, under heavy annual winter grazing, has been almost completely replaced by *Chrysothamnus stenophyllus*. Yet, under extremely heavy use, alternating annually with rest, it has increased and suppressed *C. stenophyllus*.

On the uplands of the fan, *A. spinescens*, the species that declined in all spring-grazed pastures, has almost disappeared on the area grazed every year through the winter and early spring. Under heavy alternate-year grazing (midwinter), *A. spinescens* has increased. On the unit grazed every year, the shrub cover is a nearly pure stand of *Eurotia lanata*, except in the slight hollows where *C. stenophyllus* has replaced *A. nova*. This upland site is similar to Pine Valley (table 1) in that desirable species have not been replaced by undesirable species. However, as in Pine Valley, the perennial cover here is weak and annual weeds are abundant and thrifty in years when conditions are favorable for their growth.

On the unit grazed in alternate years, *E. lanata* grows in association with *A. spinescens*. Here, annual weeds are restricted to sites disturbed by small mammals.

Although two different plant communities exist in Antelope Valley as a result of the two grazing treatments, they are about the same in total productivity of desirable species and of usable forage as shown here:[4]

	Grazed every other year (Lb./acre)	*Grazed every year* (Lb./acre)
Grass	14 (16)	14 (16)
Artemisia (2 spp.)	36 (40)	2 (2)
Eurotia	68 (76)	108 (121)
Undesirable shrubs	25 (28)	43 (48)

As sheep range, the area grazed in alternate years is the more desirable. It offers variety, and the *Artemisias* are nutritionally superior to *Eurotia*.

Processes of change

Grazing management depends for its success upon an understanding of processes in the successional ecology of particular range types. Some processes of change are so universal as to be considered general ecological principles. Others may be less widely applicable--rather regional and more closely related to particular range types or dependent on characteristics of the various individual species.

Alleviation of grazing pressures that have induced compositional change in a community does not immediately and by itself terminate or reverse a change that such pressures had induced. Many plants, desirable and undesirable, are long lived. If increase of undesirables is related to only a weakening of the predecessor species,

[4]Values in kg./ha. shown in parentheses.

relaxation of grazing sometimes does permit plants of the original cover to regain their competitive status and suppress the invaders, but such rapdi recovery can occur only where prior grazing has been harmful for a comparatively short time. Where plants of the original species have died, recovery depends upon establishemtn of seedlings. Although mature plants reinvigorated by reduction of grazing pressure might suppress a successor species, it is only under the most favorable of conditions that seedlings of the former species can become established in competition with the successor.

On the deserts, where amount and season of precipitation are so erratic, years of good seed production are infrequent for most psecies. Years favorable for seedling establishment are also infrequent, so the circumstance of a good seed year followed by a good establishment year is a rare occurrence. If a range is to recover within a reasonable period (a decade or two as compared with a century, perhaps), it seems that some kind of catastrophic condition or event is needed to activate the recovery. Of course, such an event would have to be relatively less favorable in its effect on undesirable than on desirable species. The deterioration brought about by harmful grazing is itself an example of catastrophically-induced cover change; however, in this case, the change is in favor of the undesirable species. Unlike other catastrophic events, grazing pressure is controlled by man, and it persists until alleviated by man. None of the others are of long duration, but their effects might be.

Catastrophes favoring range recovery are not uncommon on the desert; it is through their action that much of the improvement we have cited took place within such a remarkably short time. Among these unpredictable events, extended drought is the commonest and occurs most frequently.

Insects in epidemic numbers have materially weakened or reduced stands of established plant species. Insects might favor either desirable or undesirable forage species, but our limited experience suggests that the dominant species of the pristine vegetation of the salt desert--generally the more desirable species--are less susceptible to insect damage than are the disturbance species. We think insect damage to *Chrysothamnus stenophyllus* might have permitted much of the increase of *Artemisia nova* at Newark (fig. 2), at James, and possibly at Antelope.

Fire is not the important influence that it is in the semiarid and subhumid regions. Productivity is too low and plants are too widely spaced for fire to spread.

We think *Atriplex confertifolia* has become a much more important constituent of many cold desert communities than it was before exploitation of the range. *Atriplex* is less well adapted to endure extended drought than are its more desirable associates *Eurotia lanata* and *Artemisia nova*. Many *Atriplex* plants die when one dry year follows directly upon another. The plants that remain lose large portions of their crowns. When conditions again become favorable for new plant establishment, some of the voids formerly occupied by *Atriplex* can be filled by the other species if grazing conditions permit (fig. 3, left, and table 1).

Of course, some of the drought-caused openings will be occupied again by *Atriplex* seedlings; so, drought-recovery change is only partial. Successive cycles of extended drought followed by favorable growth years are needed to undo the vegetal change effected by harmful grazing. In the eastern Great Basin, the average period of such a cycle may be about 15 years. Compositional change under protection or under grazing treatments favorable to range improvement, then, is not linear with time as our diagrams here show it to be. The species components of the cover remain more or less static in relation to one another for periods that are separated by other periods during which compositional relations undergo comparatively rapid change.

Special approaches to studies of competition and succession in shrub communities

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Shrubs do not exist on wildlands as solitary individuals or monospecific stands responding to independent factors of environment and types of use. Instead they are components of complex plant communities responding to a multifactored, holocoenotic environment. Furthermore, they function in ecosystems contributing to the energy flow, nutrient cycling, and ecosystem control through modification of the microenvironment.

Shrubs routinely dominate seral communities or occur as understory in areas that have a successional potential for forest or woodland vegetation (e.g., Skau and others 1970). They also are common where historical perturbation of the landscape has seriously altered the potential for more lush vegetation, allowing development of a shrub-dominated plagioclimax (Eyre 1963). As examples, we can cite the moors of Scotland and the expanded macchia of South Africa where shrublands have replaced former forests. Grasslands also have been invaded by shrubs where overgrazing and/or fire exclusion have been strong environmental influences (Shubert 1969).

Whatever the successional status of the vegetation considered, the success of shrubs depends on their competitive abilities. No autecological or physiological data can completely explain why a plant naturally grows where and when it does without appealing to competitive effects necessarily operative in a community or ecosystem context (McIntosh 1970). Accordingly, our efforts in other realms of shrub biology are valueless unless we relate them to appropriate synecological contexts in space and time.

Competition

Competition has been defined traditionally as the process occurring when the immediate supply of a single necessary environmental factor falls below the combined and simultaneous demands of the plants living on a given site. This concept is generally adequate in considering such environmental resources as mineral nutrients, water, and light. However, many recent discoveries of allelochemic effects (Tukey 1969; Muller 1969; Whittaker 1970; Went 1970; Whittaker and Feeny 1971), especially prevalent in relation to shrubs, lead us to recommend the use of Harper's (1968) concept of "interference" as a more inclusive and realistic way of dealing with plant-environment interactions. Harper (1961) defines interference as "those hardships which are caused by the proximity of neighbors (usually other organisms feeding at the same trophic level)."

Unfortunately, most research on competition or interference has not been done with perennials and particularly not with shrubs (Knapp 1967). It is extremely difficult to get statistically reliable data in field experiments involving manipulation of naturally established shrubs; it is even more difficult to get realistic responses from plantings. Even with careful design, data collected over a decade or so are necessary for shrubs on arid sites because of slow responses and highly variable climate.

Because of the lack of such data, we shall have to try to extrapolate some principles from herbaceous (mostly annual) species and tree-related literature.

The intensity of competitive interaction between shrubs is conditioned by (a) inherent qualities of the competing individuals, (b) the interacting plants in the community, (c) animals that affect the vigor of the competing individuals, (d) the abiotic environment, including natural catastrophic events such as fire and storms, and (e) man's interjections into the environment.

The shrub life form has many advantages in certain environments. For instance, a shrub has less energetic and nutrient investment in aboveground structure than a tree. The structural modifications affecting light interception, heat dissipation, and transpirative losses vary widely depending on the species involved. Leaf configurations and longevity are especially important in these functions. Drought deciduousness is more common than evergreenness, the more arid the site involved (Mooney and Dunn 1970a). Depending on the soil and climate of the site, the multistemmed form of shrubs can greatly influence interception and stem flow of moisture, aiding or hindering it from infiltrating further into the profile than under herbaceous plants (Mooney and Dunn 1970b; Slatyer 1965; Specht 1957a, 1957b). Although species and sites differ greatly, many shrubs can get their roots down quickly, form an extensive root system, and utilize moisture deep in the soil profile. This characteristic partially explains why shrubs are more successful than trees or grasses in climates where major soil moisture recharge comes during the nongrowing season or very erratically, as in extreme deserts. Although this is usually advantageous to man, this characteristic is also exemplified in our most troublesome phreatophytes. A probable record depth of rooting, 175 feet, has been ascribed by Phillips (1962) to *Prosopis* in southern Arizona.

Shrubs do not usually have high shoot-root ratios. This means that comparatively less aboveground biomass is drawing nutrient inputs. Shrubs have comparatively greater root surface than trees. Although root densities may be less than those of competing grasses, the shrubs' perennial nature may allow immobilization of more of some limiting nutrients and slow the nutrient recycling process, favoring further shrub invasion of grasslands. This would be doubly effective when combined with evergreenness, which limits the rate of nutrient cycling even further (Monk 1967).

The longevity of shrubs is an advantage by enabling them to persist and compete on a given site. Christensen and Brown (1963) tallied more than 400 growth rings on an individual *Coleogyne ramosissima*. Cottam and others (1959) estimated that some *Quercus gambellii* × *turbinella* clones in central Utah may approach 4,000 years of age.

Reproductive capacity is always a definite competitive advantage (Salisbury 1942). Except for a relatively high frequency of vegetative reproduction, shrubs as a group probably display no particular differences from other plants in this regard. Many examples of greater seed production, delayed germination, germination polymorphism, unique germination requirements, efficient mechanisms for seed dissemination, and food reserves connected with reproductive success could be detailed; however, sufficient examples are cited in the other papers in this volume.

The considerable effects that diseases, insects, and other invertebrates may have in changing competitive vigor and altering shrub-dominated community composition have not received attention commensurate to their effects. However, Furniss and Barr (1967) have shown how a butterfly larva (*Anacamptodes clivinaria*) can cause considerable changes in *Cercocarpus ledifolius* shrublands. Tent caterpillars have decimated many acres dominated by various shrubs of the Western United States (Stetzer 1968). For instance, Stanton (1959) noted their extensive alteration of *Purshia tridentata* stands in eastern Oregon. West has observed their considerable damage to *Prunus fasciculata* in the Mohave Desert and also has seen extensive damage by round-headed woodborers (Cerambycidae) to populations of *Atriplex*, as first reported by Hutchings (1952). Cutworm larvae (*Agrotis orthogonia* Morrison) also cause problems for this genus.

Perhaps the best documented example of widescale shrub destruction is that by the webworm moth larvae (*Aroga websterii*) on stands of *Artemisia tridentata* in the Western United States (Hall 1963). This insect has changed the vegetation from shrub-dominated steppe to grassland within several years. The end result is a vegetation change equal to that seen after herbicidal or prescribed burning applications. Much more invertebrate influence on shrub growth will be noted when more trained observers are available to study these interactions.

Similar oversight has been noted for microbial and allelochemic interactions in plant competition. We have noted some studies of germination inhibition from *Artemisia* (Reid 1965) and *Adenostema* litter (Naveh 1960), and volatile inhibitors from several soft chaparral genera (Muller and others 1968; Muller 1970). However, the efficacy of these allelochemics remains to be completely verified under field conditions. Rood (1970) and Bartholomew (1970) contend that the bare zone around shrubs in Argentina and California, respectively, can be explained by activity of small mammals.

Went (1969) advances the argument that competition is insignificant in reducing the number of reproducing plants in arid environments. He feels that inhibitors do not reduce competition, but rather restrict growth of the desert shrub itself. This is essential for desert survival--so as not to absorb the total soil moisture storage, leaving some for use during the long intervals between replenishment. He concludes that it is not mutual competition that eliminates excess plants, but the ability of the environment to support them. This provocative idea hinges on definitions and severity of environment. We acknowledge with McGinnies (1969) that conventional competition may not operate between the widely spaced shrubs in extreme deserts; however, elsewhere in shrublands it appears that competition is approximately inversely proportional to the square of interplant distance (Goodall 1960). One should not automatically assume that open-spaced shrub vegetation is subject to minor competitive pressures, for these communities are often effectively closed by considerable belowground root interference.

Simply the number of individuals does not always give a reliable indication of the success of a plant species, since under good conditions there may be fewer plants per unit area. This is because the more vigorous individuals develop rapidly and thereby exclude the weaker ones; this results in a lowered density. The test of competitive success is the plant's ability to reproduce.

Severe competition in shrub establishment, especially from annuals, has been widely noted (Litav, Kupernik, and Orshan 1963; Holmgren 1956). Some species suppress others more if they are themselves aggregated (Watt 1955) but not all such situations involve negative interference. In the case of *Purshia tridentata,* Ferguson (1962) and Ferguson and Basile (1967) concluded that the chance of any seedling's surviving until the end of the growing season increased as the number of seedlings emerging per spot also increased. West (1968) observed enhanced survival of this shrub in natural seedling clusters from rodent caches. This could be explained by the creation of a beneficial microenvironment, where several seedlings grow together. Gasto (1969) found that although seedlings of *Atriplex confertifolia* and *Eurotia lanata* emerged irrespective of mature plants, the only significant survival of seedlings of these species was adjacent to large individual shrubs.

Shortage of a factor does not necessarily imply competition. All individuals of a desert shrub community may be short of soil moisture, but if the environment of each plant is independent of that of its neighbor, then there is no real interference in the growth of one plant by another. Donald (1963) stated that there are probably few instances where plants actually compete for space *per se;* however, evidence is mounting that the lack of "safe sites" for germination can be a limiting factor in many communities (Palmblad 1968).

Finally, we need to learn how shrubs and the communities they dominate react to man's old treatments, such as grazing and fire, and to the newer manipulations and pollutants. For instance, Cooper and Jolley (1969) predict some general community readjustments following weather modification. We do not have enough autecological or synecological information to predict what specific changes are likely to result in shrub-dominated communities if climate is altered. Already underway are studies of how the Los Angeles Basin chaparral is reacting to pollution. Pollution tolerance ratings for horticulturally important species have been established. Such knowledge is useful in advising about shrub plantings for urban open space and highways. Similarly we need to know how wildland shrubs react to such new disturbances.

Interpreting interference involves numerous considerations. Our ecological experience cautions against accepting the single-factor reasoning that surfaces all too easily. The ideas of competition for water and nutrients are only part of what we need to consider in explaining why a shrub flourishes or does not. Shrubs use many different strategies in coping with a given environment.

Succession

Although perennials such as shrubs usually maintain more or less similar populations from year to year under any particular and continuing type of environmental influence, including management, neither the community nor the physical environment is static when viewed over the long run. If environments are modified either externally or through the effects of the plants themselves, the resulting sequence of vegetational changes is called a "successional pattern." Species or individuals are replaced because others are presumably better adapted and therefore can more efficiently utilize the changed or changing environment. Knowledge of these patterns is demonstrated by everyday use of range condition and trend evaluation for management of livestock and game ranges.

The microclimatic changes accompanying succession are most often pointed out, but allelochemic influences also function in succession. Most allelochemics affect interspecific competition, but autotoxicity is by no means rare. Self-toxicity may be no serious disadvantage for successional species, however, since these are temporary residents that dominate a community for a limited time in a given place. Inhibition of nitrogen-fixing bacteria and mycorrhizal fungi (and thereby of the trees dependent on them) by substances from the heath, *Calluna vulgaris* (Harley 1952), is a striking example of the effects of secondary substances on the microbial community of the soil and thereby the total successional pattern. In other cases, shrubs may be an essential link in the successional processes of forests by building up soil nutrient levels, especially of nitrogen, to the point where trees can thrive (Skau and others 1970; Zavitkovski and Newton 1968).

Although classical approaches to studying succession have yielded plentiful understanding of shrubland vegetation dynamics (Daubenmire 1968), there is a need for faster and easier ways of detecting and interpreting succession.

If plant communities are the net result of the total competitive process, the interaction between and among species suggests that pattern of distribution may provide information about competition and succession. Positive association at small scales is relatively rare and can generally be explained in terms of similar habitat requirements in areas where environmental pattern has a very small-scale effect or by common exclusion of the associated species by a third species. Negative association is much commoner, but can generally be explained by competition or the physical impossibility of two or more individuals growing in the same place at the same time.

Conventional wisdom would lead us to hypothesize that increasingly intense competitive pressures would develop as crowding intensifies during succession. Many have thought that the resulting spatial pattern might tend toward a more regular than a random dispersion pattern in shrub communities, particularly in arid regions. However, only a few papers discussing this are based on quantitative data. Cottam (1955) detected regularity in some shrub stands in the deserts of Utah and Arizona. Greig-Smith and Chadwick (1965) investigated pattern in *Acacia-Capparis* semidesert scrub in the Sudan but found no evidence of regular pattern resulting from competition between individuals for water. However, they found evidence of competition between seedlings and between smaller individuals of *Acacia* that might result in more regular spacing in older stands. Pidgeon and Ashby (1940), Anderson (1967), Anderson and others (1969), and Anderson (1971) similarly did not find general regularity in *Atriplex vesicaria* and *Kochia pyramidata* populations in Australia. A more detailed analysis of an *A. vesicaria* stand by size classes (Anderson 1970) indicated a reduction in intensity of pattern as age of the population increased. Perhaps, by random elimination of older individuals, a random distribution results from a previously more strongly patterned population. The scale of this pattern may be associated with biogenetically derived microtopography and concomitant soil chemical differences. Beals (1968) in Ethiopia also found different patterns for larger and smaller shrubs of *Cadaba rotundifolia*; and McDonough (1965) found that *Opuntia* populations changed from aggregated to random--an effect that he ascribed to selective action of a lethal factor. Woodell and others (1969) found that pattern of 12 stands of *Larrea divaricata* in California tended to be clumped at high rainfall levels but regularly spaced at drier sites. Barbour (1969) found that *Larrea* in the Mohave and Sonoran deserts usually was regularly distributed whereas those of the more mesic Chihuahuan stands usually were distributed in aggregations or at random. Significant noncentral tendencies in age distribution of most stands indicated that germination and survival are rare events, contributing to stands of one or several age classes. Turner (1962) investigated the distribution of *Larrea* and *Franseria* in the Sonoran Desert near Phoenix, Arizona; from tests of geographic homogeneity and Poisson distribution he concluded that *Larrea* was randomly dispersed, while the variance/mean ratios for *Franseria* suggested that it was overdispersed (tending toward regularity). Wright (1970) showed that individual *Larrea* plants were contagiously clumped into small-scale mounds at eight sites in Avra Valley, Arizona. The mounds were contagiously distributed on a larger scale. All these studies either did not consider or could not account for grazing history variabilities or other disturbance phenomena affecting successional status of stands.

An ungrazed area in western Nevada studied by Tueller had some *Sarcobatus baileyi* distributed at random. At a grazed site in the Mohave Desert, he found *Yucca brevifolia*, *Y. schidigeri*, *Y. baccata*, *Opuntia bigelovii*, *Ephedra nevadensis*, *Coleogyne ramosissima*, *Larrea divaricata*, and *Ambrosia dumosa* all randomly dispersed. Anderson (1961) showed how scale of pattern for *Vaccinium myrtillus* and *Calluna vulgaris* could be related to the effects of historical tillage and present grazing and treading of sheep as the latter affected soil aeration. West and Baasher (1968) found both recently grazed and protected stands of *Eurotia lanata* had random dispersions of the shrub populations, at different scales, whereas two *Atriplex falcata* populations--one protected from grazing for 10 years inside an enclosure and a recently grazed stand--both showed a trend toward regularity, also at different scales. McConnell and Smith (1970) studied the effect of grazing on dispersion of *Purshia tridentata* across fencelines separating uniform sites that had different grazing history. The large increases in mean area per plant that developed under heavy grazing did not alter the overall form of random dispersion. In a comparison of heavy versus moderate use, inclusion of 1-year-old plants on the moderately grazed area (10 percent of population) caused aggregation of the population. Even though a larger number of 1-year-old plants (22 percent of population) occurred in the heavily grazed area, the population remained random. The contrasting reaction probably resulted from a differential pattern of seedling mortality due to different amounts of herbaceous understory in the shrub-dominated communities.

Since investigators have used widely varied methods for testing dispersion patterns, comparison is difficult. Also because of the many confounding elements of microtopography, and taxonomic and structural differences in the reproductive habits of shrubs, it is impossible to conclude now whether generalizations can be made about how shrub dispersion patterns change with successional status.

Equally inconclusive statements can be made about the generality of large-scale community patterns. Although sharp demarcations between communities can be seen, especially where topographic and/or edaphic changes are sharp, the changes in species composition and dominance in other shrub-dominated vegetation types are rather gentle, particularly where man's disturbances have complicated the use history of an area. In comparing the *Acacia*-dominated communities of two Ethiopian fault scarps of different steepness, Beals (1969) found species distributions and dominance tended to be more sharply demarcated where the environmental gradients were steepest. From this it could be hypothesized that the more the environment varies in space and time, the more often communities are dominated by one or a few species and the easier it is to delineate community boundaries. However, this hypothesis would not be supported by results of Fisser's (1965) comparison of the abundance of four *Artemisias* on two mountain ranges in Wyoming. The gentler Owl Creek gradient (14-percent slope) had each sagebrush species as the sole community dominant over at least a 100-m. elevational belt, whereas all four species grew in stands of mixed dominance on the steeper slopes (23 percent) of the Wind River Mountains. Fisser's findings perhaps excepted, we can state that harsher environments, having fewer species to begin with, have a greater chance of developing monotypically dominated stands and alternes because of less biological mediation of physical environment and accentuated competition where species do meet (Nytzhenko 1948). Largely because shrubs either prevail in more hostile environments or are parts of successional mosaics in areas of greater precipitation, and the above relations generally hold, we tend to see shrub synecology handled more often in a unit-association manner than by the continuum approach.

Although grazing has been a major well documented factor influencing competitive advantages and altering succession (Ellison 1960), considerable contradiction prevents us from generalizing on how grazing pressure influences diversity and stability of communities (Harper 1969). Equally complex reasons account for the various interpretations of the effects of fire, unless autecological information is also in hand. It is best if autecological and synecological studies are pursued concomitantly so that results from both areas reinforce their respective progress.

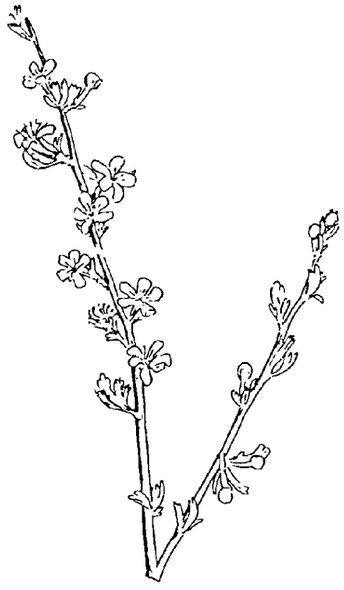
Many have puzzled over why plants, in the face of depredation by countless animal consumers, are dominant over much of the land's surface (Wiegert and Owen 1971). Although animals may be limited by factors other than their food supply, also important is the fact that not all plants, or at least not all their parts, are palatable. The woodiness of shrubs limits what vertebrates, at least, can thrive on. Furthermore, the evolution of thorns and spines has probably helped save some shrubs from extinction or, at least, given some measure of competitive advantage. This heavy metabolic investment in woody and protective tissue formation explains why shrubs produce generally less forage for vertebrates with less efficiency than herbaceous plants.

Because of the holocoenotic principle, it has been arbitrary for us to consider shrubs rather synonymously with community herein. Very infrequently do shrubs make up the sole vascular plant component of the community. The interactions between shrubs and overstory and/or understory competitors can be commonly very important in determining successional patterns. For instance, shrubs may serve as "protectors" of trees or understory herbaceous plants. Grasses frequently retreat under the cover of shrubs, especially spiny ones, when grazing pressures increase. From these protected niches they may produce propagules for reinvasion of the interspaces when grazing pressure lessens. In drier environments, shrub cover commonly provides a more favorable microenvironment and interspaces may be naturally bare of herbaceous cover.

During wet years or in more mesic environments where herbaceous cover is continuous between the interspaces and beneath shrubs, fire is commonly carried, usually differentially reducing the shrub cover. This protectiveness of shrubs can thus on occasion serve to the adverse effect of the shrub population.

Finally, the stochastic element of succession should not be overlooked (Jameson 1970a). The probabilities involved in a plant's longevity and reproductive activities combined with the chance of propagules being present when favorable environmental conditions exist greatly influence the history of a stand. Irregularity of some environmental variables disrupts stability and complicates predictability of successional patterns. For instance, the noxious half-shrub, *Gutierrezia sarothrae*, a common increaser on southwestern United States ranges, was assumed to flourish when the palatable competitors were overgrazed. However, Jameson (1970b) has recently shown that the vagaries of climate are more important than grazing in explaining the waxing and waning of its populations.

Because of almost an infinity of possible factor interactions at the real world-ecosystem level, the shrub biologist must constantly keep aware of what synecological context he wishes to extrapolate to or from. His ability to relate other information in or to landscape units will determine his success at understanding and managing lands where shrubs are important ecosystem components.



Some perspectives on shrub/environment interactions

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The anticipated title of this essay was originally "Shrub response to climate, soils, and topography," a subject which evoked in us a good deal of agonized reflection. However, we decided that our new title--although perhaps a little offbeat--potentially lent itself to more effective orchestration. The basis of the consideration that led to this decision also illustrates the reasoning that culminates in our initial conclusions.

The physiognomic term *shrub* is frequently defined as "a woody plant not more than 30 inches high, much branched to the ground" (e.g., Willis 1960). This description scarcely permits a distinction between some fastigiate trees (e.g., some spp. of *Populus*) and those plants that produce short, twiggy annual branchlets from a perennial rhizome (e.g., *Parinarium capense* (Rosaceae)). The apparent morphological discontinuity between trees and herbs is bridged by a continuum in size, in woodiness, and in morphology, as witnessed by the various references in the literature to "woody herbs," "suffrutices," and "obscurely shrubby."

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Shrubs are a heterogeneity of growth form that may have very diverse evolutionary origins; these origins might well help to explain the widespread geographical distribution of shrubs among the earth's environments and vegetation types. Shrubs are found throughout a wide range of latitude, from the high arctic to the tropics; from sea level to high alpine elevations; in littoral (and even offshore reef) communities; in coastal heath; in forests, whether temperate or tropical, mesic or semiarid; in semidesert steppe and arid desert; in shaded or open habitats, on mineral or peaty soils, on soils that are acid, alkaline or salt-affected, fertile, or impoverished. What price the possibility of generalization then when shrubs exhibit such a virtually cosmopolitan distribution and an ecological ability to occupy most niches with which we are familiar?

The sense and utility of our questioning must depend largely on the scale of our inquiry. In the context of synecological studies, this scale might be at the level of association types if we are primarily concerned with comparisons that bear on the apparent similarity between shrublands of Mediterranean climates; alternatively, we may be more interested in the structural organization of individual shrublands, with a view to their successful management; or we might be interested in competitive or ecophysiological processes that operate between shrub individuals. These different kinds of problems not only require different kinds of questions to be asked, but also very different scales of investigation within which such questions--and hopefully, their solutions--are necessarily constrained.

These considerations lead to our initial conclusions, which follow:

1. Shrubbiness is demonstrably an ecologically successful phenomenon in a wide variety of ecological niches, but this is of little intrinsic interest to us, because this success can be anticipated from the undoubtedly geologically long and diverse evolutionary history of shrubs; and

2. We need to constrain our scale(s) of inquiry if we are to pose meaningful questions that can lead to useful and widely constructive solutions because at best we can only deal with a space/time slice of vegetation in most of our investigations.

In this paper, we have curtailed our potential field of inquiry to examining the response of shrubs to their environment, both past and present, in three different ecological situations. We have also attempted to examine some of the widely-held generalizations that relate various plant or community "adaptations" to environmental parameters.

Boreal heathlands

The advent of palynology as a precise tool in Quaternary research, together with analyses of macrofossils and of artifacts and the possibility of developing C_{14} dating, has provided ecological historiographers with a wealth of evidence for vegetational change (at least in northern latitudes) during the last 15,000-16,000 years. The broad chronologies for both Europe and North America in Late- and Post-glacial time are too well known to bear repetition here, but the detail of one or two examples of heathland development do warrant some further emphasis.

The pollen of *Calluna vulgaris*--a dominant ericaceous shrub found in the heather-moor of the Scottish Highlands, the Pennines, and Breckland--does not become abundant in the stratigraphical record for Breckland until about 3000 B.C., although fossil remains of dwarf shrubs, such as *Salix herbacea* and *Dryas octopetala*, are abundant in British Late-glacial deposits. Only 20 years ago, Godwin and Tallantire (1951) demonstrated conclusively that this *Calluna*-dominated vegetation developed after this East Anglian region had been covered continuously by forest for approximately 4,000 years; this decline in the forest was associated not so much with significant climatic shifts, as with forest clearances initiated by Neolithic people. As a result of continued anthropogenic pressures, these heaths remained open and, indeed, expanded during Iron Age times; subsequently, for almost 900 years they were influenced by countless generations of rabbits. This broad pattern of events is common in much of Britain, and evidence of charcoal from many shrub species first occurs in deposits dated to Neolithic and Bronze Age times (Godwin 1956).

In the Southern Pennines, Conway (1947) has shown that deforestation on the sandstone uplands did not occur until the time of the Norman incursion; in a real sense these moorlands are a legacy of an earlier Normandy invasion, although their persistence as homogeneous, even-aged, monocultural stands derives from the medieval practice of moor-burning, which was adopted and has been used intensively by game-keepers as an aid to grouse-rearing since the 19th century. Grouse moor is generally burned, in wide strips, at regular intervals of from 7 to 15 years. After a burn, the heather usually resprouts from woody rootstocks that are buried in the peat and that usually survive all but the most severe burns. Throughout Britain and mainland Europe, large tracts of heath-moor bear silent testimony not so much to climatic or edaphic constraints in their environments as to man's use (or abuse!) of those environments.

Furthermore, this overall pattern on a broad community scale is recapitulated at a much smaller scale. Watt (1955) has shown that the normal mosaic of a mature, relatively undisturbed *Calluna* community is made up of uneven-aged individuals that, using his terms, represent "pioneer," "building," "mature," or "degenerate" phases, linked as elements in a natural cyclic process. This process has been confirmed not only for this community but for other shrub species or shrub mosaic patches in a variety of environments (Nicholson and Robertson 1958; Kershaw 1960; Anderson 1961; Anderson 1967; Anderson and others 1969; Anderson 1970). However, persistent burning imposes a more uniform physiognomy on the vegetation; the resprouted shoots within an originally burned area are even-aged although they might have grown from an uneven-aged population of rootstocks.

The point we have attempted to make is that the status of some present shrublands might not reflect (at least on a broad scale) the exact correspondence with categorized "phytoclimates" that some plant geographers (e.g., Raunkiaer 1934; Cain 1950) have sought to establish. We are not questioning the apparent existence of a correlation between physiognomic vegetation types and regional climates, but rather the interpretation of the ecological process(es) that have led to these regional convergences. The accumulating evidence from areas of longstanding human occupation clearly demonstrates the selective influence that man--particularly through his use of firebrand, axe, and browsing animal--has had in promoting shrub dominance in some environments where today's climatic condition would have permitted forest cover to develop.

This history of selection alone cannot explain the entire basis for the ecological success of *Calluna*; its physiological reputation as an active soil podzolizer (Gimingham 1960) and its ability to successfully withstand moderate drought-stress by comparison with other potential (ericaceous) competitors (Bannister 1964a,b,c), must also contribute along with its vigorous response to controlled burning regimes to its success over a wide range of climatic and edaphic conditions (cf. Gimingham).

Subarctic birch copse and dwarf heath

The influence of climate *per se* on shrubs and shrublands may be more easily assessed in more youthful environments (those recently released from perennial ice-cover), where the influence of man's activities has been comparatively minimal. Evidence of "climatic" influences on the distribution and abundance of shrub copse and dwarf heath is provided by Anderson and others (1966) for the Skjaldfannardalur region, which abuts onto the Drangajökull icecap in northwestern Iceland--approximately 50 miles south of the Arctic Circle.

The valley of Skjaldfannardalur, which is incised into relatively uniform material of a Tertiary basalt plateau, rises from sea level to an altitude of 420 m. some 20 km. and northeastward from the sea. Despite recent climatic amelioration, the winter climate is severe and temperature inversions can cause ground frosts even during high summer. Heavy snowfalls are experienced from November to March, and the area is persistently subjected to cold, desiccating winds.

A preliminary ordination analysis of the vegetation and some physical parameters of this area indicated wind, radiation, and snow-lie regimes were important in discriminating the various facies of birch copse and dwarf (mainly ericaceous) shrub heath that occur in this valley (Anderson and others). More recently, an inosculate analysis (i.e., a simultaneous use of classification and ordination in a single program) has demonstrated that different dominant shrub types have effectively exploited the various niches created by variation in altitude, aspect, and slope in this recently deglaciated valley and that these measured parameters reflect the physical context in which the "mesoclimatic" variation is determined (Dale and Anderson, in preparation).

If this study suggests a useful conclusion in our present context, it is that physiognomically similar shrubs--most of which are related at least at the familial level (and therefore which have had a not totally dissimilar evolutionary history)--nevertheless have rather precise "dominance-ranges" within an area of relatively uniform soil and an overall, similar climate. It may suggest to the less sanguine ecologists among us that as yet we see but darkly through the glass of shrub/environment interactions.

"Mediterranean" climate shrublands

As with many vernacular words describing vegetation types, the common language terms of maquis, maccia, garrigue, chaparral, tomillares, and mallee have gained wide currency in the ecological literature. They refer to characteristic sclerophyllous shrub communities found in country surrounding the Mediterranean basin and other geographical regions having similar climates: in California, in south-central Chile, in the southern part of Cape Province in South Africa, and in southern Australia.

The striking physiognomic resemblances of these vegetation types has been a fruitful source of discussion for almost a century since Grisebach (1872) used this physiognomic similarity of geographically disjunct communities to argue the case for the dependence of life-form on climate. Curiously, Raunkiaer (1934) thought of these regions as being characterized by the large number of therophytes in their respective floras, despite the relative paucity of annuals in many Australian sclerophyllous shrublands and the statement reported in Eyre (1963) that there is probably not one species of indigenous annual in the entire flora of the southwestern Cape Province.

In many of these Mediterranean-climate regions, there is considerable evidence to suggest that at least some of these shrublands have been derived from forest in historical time, although other areas of this vegetation type are still regarded as being true climatic climax (Eyre).

Let us assume the close structural and physiological similarities that apparently exist between the five formations of sclerophyllous shrubland are a biological reality. This would lead us to argue that hundreds of species (from many distantly related families) have convergently evolved and associated themselves through a long geological history to conform to a characteristic mode. This mode is, in particular, "adapted" to an environment of cool, moist winters, and warm, potentially drought-ridden summers. Logically then, we must argue that these numerous taxa have undergone evolution through millions of years in order to adapt their distant offspring to a climatic environment that has developed only recently (geologically); this many biologists would find hard to accept, even allowing for the possibility of developing preadaptation (Stebbins 1950) or prospective adaptation (Simpson 1953).

Clearly, the originally emphatic suggestions that climatic influences have encouraged the development of convergent ecological formations may be simplistic, if this hypothesis must also encompass only some of the findings reported in recent relevant papers. In Australia, for example, Johnson and Briggs (1963) have argued convincingly for a tropical origin of the Proteaceae, a family particularly well represented in present sclerophyllous shrublands in southern Australia. It would be possible to accommodate this view within the framework of the general hypothesis by postulating recent adaptive radiation within the family (cf. Burbidge 1960), except that Specht and Rayson (1957) emphasized that most sclerophyllous members of the Proteaceae in southern Australian heaths have a summer-growth rhythm rather than the anticipated spring-growth rhythm demanded by close adaptation to an overriding climatic influence. They also pointed out that Australian sclerophyllous heaths consistently occupy very infertile soils, which they relate to the occurrence of this heath type during Pliocene times on infertile, lateritic podzols then in equilibrium with a warm,

pluvial climate that favored summer growth. Allegedly, spring-growth rhythms are the normal mode in Mediterranean climates; however Mooney and Dunn (1970) indicate near-maximum activity from April through July, months which straddle the spring/summer growth period on the "relative growth activity" of chaparral shrubs in southern California.

This lack of positive correlation between active shrub growth periods and temporal rainfall patterns is not entirely surprising for at least three reasons:

1. Growth of woody plants is typically episodic, even in those climatic regions (regions (e.g., the wet tropics) that would notionally permit continuous growth (Romberger 1963).

2. The average relative variability of monthly rainfalls in Mediterranean climates is considerable; as an example, the minimum percentage variability in the three winter months (December-February) still reaches a value of 40 for Nazareth (Israel) and a higher minimum still of 54 for the Auberry-Sierra Nevada foothills in California (Naveh 1967).

3. This temporal variation in rainfall is frequently matched by spatial heterogeneity of effective soil-infiltration, due partly to small-scale patterns in related soil characteristics (e.g., Siddiqi 1971) and partly to the redistribution of incident rainfall by way of variation in shrub morphology (cf. Slatyer 1961) and the consequent partitioning by stemflow and foliage interception to form "rain-shadows." These patterns of rainfall interception are seasonally persistent and become more important as heathland ages (Specht 1957).

A number of recently published papers (e.g., Naveh 1967; Specht 1969a,b; Mooney and Dunn 1970), which make some in-depth geographical comparisons of various aspects of sclerophyllous shrublands, illustrate the wide range of ecological complexities that are involved in what is only a superficially simple problem of ecological convergence. In this field as in others, it is abundantly clear that precise questions must be framed in the context of particular scales of inquiry if our overall understanding is to be significantly improved. It was this that enabled Siddiqi (1971) to appreciate the interrelated roles topography, water relationships, soil chemistry, fire regimes, and comparative shrub physiology play in determining the relative competitive ability and consequent mosaic structure of various shrub facies in different coastal heath types in New South Wales.

As with most ecological problems, speculation alone on the intriguing problems associated with Mediterranean-climate shrublands is a poor substitute for constructive thinking and experimentation; there is room for a master builder to create some better structural ecological edifice than now exists from the numerous bricks of knowledge at our disposal.

Arid shrublands

In many ways, words are bedevilling constructs; their limitations in expressing conceptual frameworks are no less problematical to ecologists than they are to other men. As an example, take the words "arid" or "desert" and ask a group of ecologists to define them. The only certainty is that all the (impersonal) definitions would include some statement about dryness, or limitation on water availability. By comparison, the same question put to a group of Bedouins might well elicit a similar response but one reflecting a more personal viewpoint, because there are no less than eight words in Arabic that refer to thirst of varying degrees (including one, al-Hūyam, which can also mean passionate love!).

The very description of shrublands as "arid" then, imposes on us an awareness, if not an acceptance, that lack of water is a--or the--critically important factor governing this vegetation type. This awareness has been sufficient encouragement for many students of desert vegetation to search for common physiological mechanisms among the diverse shrub forms of arid regions that will serve to explain this accommodation to seasonal and often intense drought.

We shall examine the following premises dealing with drought-tolerance mechanisms that are often cited for shrubs and other perennials (e.g., Daubenmire 1959).

1. *Development of an extensive root system that, in proportion to the shoot system, produces a low shoot/root ratio for an entire plant.*--Some desert shrubs undoubtedly develop extensive root systems. For example, *Prosopis juliflora* developed vertically to a depth of at least 65 feet according to Meinzer (1927) and *Larrea divaricata* growing in the Argentinian steppes developed horizontally to a distance of 6 m. according to Oppenheimer (1960). Garcia-Moya and McKell (1970) provide mean dry weight data, based on values for five or 10 plants, for shoot and root fractions in 13 shrub species growing in a desert-wash community in the Mojave Desert, California. We calculated the following shoot/root ratios using their data for the 13 shrubs:

Shrub species	*Shoot/root ratio*
Opuntia echinocarpa	8.09
Thamnosma montana	3.35
Krameria grayi	2.41
Larrea divaricata	2.12
Erigonum fasciculatum	2.11
Cassia armata	1.44
Brickellia incana	1.43
Krameria parvifolia	1.39
Franseria dumosa	1.38
Salazaria mexicana	1.38
Hymenoclea salsola	1.19
Ephedra nevadensis	0.82
Acacia gregii	0.76

The dry weight shoot/root ratios are less than unity for only two of the 13 species. Excluding *Opuntia*, the shoot mass is at least twice that of the root mass.

These data should cause us to pause and reflect. Can such a ratio have any physiological relevance to the process of water usage in desert shrubs? Could it not be that much of this material, in both roots and shoots, is "dead wood" which plays no effective role in terms of water transport? Perhaps it would be more relevant in such comparisons to relate the area of potential root absorption to the potential area for evaporative loss. As a crude approximation, we can examine the dry weight ratios for roots and leaves in the following eight species for which Garcia-Moya and McKell (1970) provided leaf data:

Shrub species	*Leaf/root ratio*
Larrea divaricata	0.88
Erigonum fasciculatum	0.46
Brickellia incana	0.40
Krameria parvifolia	0.39
Krameria grayi	0.30
Hymenoclea salsola	0.19
Franseria dumosa	0.18
Acacia gregii	0.05

Despite the crudity of this comparison in terms of its physiological relevance, the pattern of results is now much closer to what we might anticipate in terms of the broad initial premise; it is clear at least that the partitioning of dry weight between the primary sites of water loss (leaves) and the primary sites of water gain (roots) is generally less than unity at a particular point in time.

Development of high osmotic pressures and endurance of desiccation.--From the limited data with which we are familiar, it may be fair to assert that there is a positive correlation between the development of high internal osmotic pressures and desiccation endurance of shrubs; however, there are exceptions. The characteristic Australian semiarid shrubs *Acacia aneura* and *Atriplex vesicaria* may tolerate internal (matric) water potentials of up to -130 atm. for considerable periods between substantial rains (cf. Preece 1970; Anderson unpublished data). However, the corresponding osmotic potentials of the two species may be negligibly small in *Acacia* (Slatyer 1961) or high in *Atriplex* (Beadle, Whalley and Gibson 1957; Ashby and Beadle 1957; Walter 1962; Greenway and Osmond 1970).

An ability to reduce transpiration to an extremely low level during permanent wilting.--There is abundant evidence that plants (including those not found in arid regions!) can control the rate at which they lose water by evaporation, mainly by regulating stomatal aperture and, therefore, stomatal conductivity (e.g., Slatyer 1967). However, the concept of permanent wilting may need some redefinition for desert shrubs because there are indications that some shrubs can deplete a soil water potential far below the conventional -15 atm. for crop plants, possibly to -150 atm. or even -200 atm. (Jackson 1962; Tadmor and others 1962; Slatyer 1967).

It is clear, too, that some shrubs may utilize "marginally available" water, which is only slowly depleted by atmospherically determined evaporation (Noy-Meir 1970). The crucial role of this slowly utilized water for desert shrubs has been stressed by Kassas (1952) in Egypt, Tadmor and others (1962) in Israel, and Carrodus and Specht (1965) in Australia.

The premise "an ability to reduce transpiration" really begs the question when it is asked in respect to the range of behavior patterns shown by the spectrum of desert shrubs. Some desert shrubs (e.g., *Larrea divaricata*) are evergreen--therefore they must reduce transpiration on occasion if they are to survive--while others such as *Fouquieria splendens* become quickly drought-deciduous when water is in short supply (Cunningham and Strain 1969a). Still other shrubs such as *Franseria dumosa* exhibit a seasonal variation in the development of leaf area and leaf thickness and, therefore, a corresponding variation in rates of water loss and photosynthetic assimilation both of which are related to the availability of water during the period of leaf development. It is tempting to suppose that this behavior reflects a closer "adaptation" to prevailing environmental conditions than either of the more "extreme" behavior patterns previously described.

Perhaps it is surprising that so much emphasis in the literature has been placed on drought tolerance *per se* in accounting for the relative success of desert perennials. It may well be that an equally significant problem is the maintenance of a positive carbon balance over long periods; which would prevent the possibility of a "respiratory" death, when the effective periods for net carbon assimilation are, by contrast, extremely short. In this regard, the short but extremely high assimilation periods demonstrated for *Encelia*

farinosa (Cunningham and Strain 1969b) and the potentially high net assimilation rates demonstrated for some shrubby species of *Atriplex* (Jones and others 1970) may warrant very careful consideration.

4. *A reduction in size of leaf blades.*--We must emphasize that this premise is difficult to sustain. For example, Daubenmire (1959) noted:

> In certain plants of the desert the trend towards (leaf) blade reduction has progressed so far that the leaves are vestigial (e.g., *Ephedra*) and in still others the blades have been entirely lost (e.g., the Australian wattles, *Acacia* spp). The photosynthetic function in these plants is entirely relegated to petioles or to stems....

We fail entirely to see the relevance of this comment, because we are prepared to concede that CO_2-influx is necessarily correlated with potential water loss through the same diffusion pathway. These four premises all relate to physiological processes operating in individual shrubs; there are other premises that refer to entire communities. The following quotations will serve to illustrate the points that are frequently made:

> ...The root growth is perhaps the main biological factor operative in the organization of the (desert) plant community; the apparently open plant growth may be biologically closed due to root competition (Kassas 1966).

This generalization is frequently made in references dealing with arid environments; it also underlies the proposition that desert shrubs are uniformly distributed as a result of, or to minimize, competition for limiting water supplies (cf. Woodell and others 1969). Of the desert shrub distributions that have been evaluated in quantitative terms, the majority of cataloged distributions are either contagious or random (Anderson 1971), although there is some evidence for regular distributions in the field. Anderson has argued that uniformly distributed shrub populations probably can be developed by way of competition only when even-aged (and therefore physiologically similar) individuals are present and infiltration of rainfall is uniform. In Australian deserts, at least, it is rare to find even-aged shrub populations except in populations of *Kochia*, particularly *K. pyramidata* and *K. sedifolia* (cf. Malik 1970), and even more rare to find uniform infiltration of rainfall over any but very small areas. It could be argued that the California deserts are more arid than their Australian counterparts; however, the relative shrub densities between corresponding areas from the two continents are such that the Australian shrublands are the more arid (at least on a mean annual rainfall/plant basis), and yet exhibit no evidence of regularity.

> One of the principal reasons for the abeyance of successional phenomena (in desert regions) *is the almost total lack of reaction by the plant on its habitat.* The existence of a plant in a given spot for many years does nothing to make that spot a better habitat for some other plant or some other species. Only in the rich stands of desert vegetation is there a local amelioration of conditions due to the presence of large and long established perennials (Shreve 1942).

Although we do not wish to argue for or against succession occurring in arid vegetation, we react strongly to Shreve's (1942) suggestion that desert plants do not react on their habitat. There is now strong evidence that desert shrubs impose soil (chemi-

cal) patterning (e.g., Rickard and Keough (1968) for *Grayia spinosa, Sarcobatus vermiculatus*; Malik and Anderson (1971) for *Atriplex inflata*) and that some desert shrubs produce allelopathic materials (e.g., Muller 1953; Evenari 1961; Whittaker 1970). These may be significant determinants of some arid vegetation mosaics. Too, Charley and Cowling (1968) showed that the main nutrient reservoir of arid-zone soils is confined to the surface few centimeters of the soil profile. Inasmuch as much of this potential reservoir is transported and fixed into woody biomass, its recycling period must in part be dependent upon the rate and pattern of internal retranslocation and the overall generation time of individual shrubs.

Discussion and conclusions

A hurried, brief review of some perspectives on shrub/environment interactions inevitably will be construed either as an admission of our own corporate ignorance or as an attempt to create a side-stall at an ecological fair, wherein we have set up various "Aunt Sallies" only to experience the pleasure of a brief shy. Neither interpretation would do justice to our intent. Inadequate though our arguments may be, they do reflect a desire to understand and resolve the many inconsistencies that currently exist in our ecological understanding.

There are few universal truths to be made regarding shrubs, except to say that there are few habitats or niches for which some shrub or other does not seem to be well adapted. For this Conference, at least, this may be an acceptable and pleasing conclusion. Clearly the perennial, woody shrub habit has both advantages and disadvantages in any given ecological situation. Potentially it can be a valuable source of long-term stability of vegetation cover in those environments that exhibit climatically and edaphically extreme oscillations. It may contribute to a regulation of recycling rates, particularly of soil nutrients. By its nature it is potentially more plastic in its morphological response, particularly to such intermittently but intense selective forces as fire, grazing, and drought. But there may be associated disadvantages and limitations, too, depending on one's point of view. The ecological success of *Lantana* as a weed colonist in Hawaii and other Pacific Islands may be a disadvantage to cattle farmers; mature or degenerate shrublands elsewhere may imply a secured capital reserve of nutrients that is not being recycled sufficiently quickly for a potentially maximal productivity to be maintained.

Our major concern, however, is more general and one that transcends our topic, although it stems from our topic. It would be difficult to deny that there are some inconsistencies in regionally-based generalizations made concerning shrubs and shrublands. If our concern is to develop a rational and integrated vegetation science, we must accommodate these inconsistencies in a better textured framework of understanding than now exists. Perhaps our primary problem is to identify the reasons that cause the obstructions and delay in providing this necessary, conceptual integration.

It would be simple to suppose that individuals or "schools" of ecologists necessarily operate on the basis of their past training and immediate experience, so that the *kinds* of questions asked in ecological studies may be very different. Major (1961), for instance, has polarized the situation in quantitative ecology thus:

> The one group uses mathematical analysis to investigate the ecology of unclassified vegetation; the other uses mathematical analysis as an aid to classifying vegetation whose ecology is unknown. In the former case the outsider cannot be sure *what* the authors are talking about; in the latter case he cannot be sure *why* they are talking about it.

Clearly Major has a point, but he could have gone further by emphasizing the links that often seem (to us) to bind a particular *philosophy* of questioning and problem-solving technique to the scale of the problem being studied. Put crudely, we see a major discontinuity between the innately holistic philosophy that is necessary to examine a problem on a broad scale (with its associated richness of interactions, networks, and massive heterogeneity) compared with the essentially mechanistic philosophy of ecologists who seek to solve problems at a smaller, more local scale, where the associated reduction in heterogeneity is sufficient to allow interpretations set in a physicochemical (or purely formal, mathematical) framework.

A primary error in much modern ecological work is the supposition that one or other philosophical approach is self-supporting and internally adequate, irrespective of the scale of the problem being tackled: a supposition that leads to the danger of viewing vegetation/environment relationships through the eyes of an artist, so producing a perspective that is more likely abstract rather than real.

There should surely be a continuum of ecological interest and endeavor between these extreme viewpoints and, therefore, an appreciation of the wider implications of our individual approaches and their philosophical shortcomings that are implicit in our efforts to produce a well-structured, integrated hierarchy of ecological knowledge and understanding. Perhaps too, we should expand our conventional horizons and recognize the significant advances that are now being made in biochemical ecology. This subject has been reviewed, in terms particularly of allelopathic materials by Whittaker (1970), but the recently reported work on the potentially adaptive nature of conformational flexibility in enzymic proteins in relation to temperature extremes (e.g., Levitt 1969) or variation in soil chemistry (e.g., Woolhouse 1970), is worthy of serious appraisal.

Certainly we cannot close our eyes to past inadequacies, any more than we can do the same to future prospects. If we expose ourselves to some intellectual discomfort in the process, at least we have indicated that a very worthwhile challenge remains to be accepted.

The role of shrubs in nutrient cycling

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An ecologist may ask two general kinds of questions concerning any assemblage of plants, animals, and soil. First are questions relating to general structural and constitutional characteristics where the usual concern is depiction of the system as an agglomeration of names and numbers representative of the landscape unit at a chosen point in time; the creation of a static likeness in field and laboratory notebooks in order to throw light on *why the system is as it is*. Second are questions directed at internal functions that condition the external display and regulate its temporal change; these may focus on segments or on the system as a whole, but they are all concerned with *the way the system works*.

It is fair to say that the main concern of field ecology in the past has been with basically static descriptions and explanations of local and regional differences between biotic units in terms of one or a few major environmental variables. Increasingly, however, there is a move to studies of processes and clarification of the ways in which these mesh in the overall pattern of community function. Such change in emphasis is apparent in most ecological work of the last decade but particularly so in studies of water relations and energy exchange, both of which have derived much impetus from advances in research in crop physiology. Mineral cycling, on the other hand, has been relatively slow to change, and it is only fairly recently that more attention has been directed to the dynamics of turnover at a finer level of study than that of the annual cycle where litter fall is taken as the basic currency and measure of activity. This is not to imply that the general field has been neglected. To the contrary, there is a voluminous literature well covered by a series of recent reviews (Ovington 1962, 1965, 1968; Rennie 1955; Nye and Greenland 1960; Egunjobi 1969) that deal with both litter production and aspects of mineral cycling, and others such as the paper of Bray and Gorham (1964) that are concerned with litter alone. The most comprehensive work to date is the world summary by Rodin and Basilevich (1965), which brings together all information on production and mineral turnover published prior to 1965.

This literature is both geographically and biologically diverse. It is, nonetheless, heavily weighted toward ecosystems of humid regions; tropical vegetation is well represented, so too the forests of temperate and subtemperate areas; but out toward semiarid and arid conditions the information available is limited, fragmentary, and deals almost exclusively with gross quantities of nutrients held in biomass and the amounts deposited annually in litter fall. Here as elsewhere the tendency is to neglect static and functional studies of the soil and the biological activity which proceeds there. This is regrettable, particularly when it is known that transformations and transports of nutrients which occur in the substrate play a decisive role in determination of mineral flux through the components of biomass.

In view of this deficiency, the bulk of the present paper deals with those aspects of soil nutrient distribution and system physiology, such as soil biology, which usually are lightly treated but which do much to determine temporal and spatial variations in nutrient flows of any community, but particularly shrub-dominant ecosystems.

Site mineral capital

The phytomass component

As with most ecological studies, mineral cycling may be approached at a number of levels of detail. Firstly, and as is commonly the case, turnover may be looked at from the point of view of the annual cycle of deposition in litter, and this throughput can be examined against the background of phytomass mineral content. Studies of this kind are legion (see Rodin and Basilevich 1965) and have done much to highlight important aspects of mineral involvement in plant production and describe qualitative and quantitative differences between major vegetation types representative of the broad climatic zonations of the world. Thus the summarized data of tables 1 and 2 give an overall picture of the way in which phytomass and litter mineral content vary with climate and how the amount and throughput of N change from arctic to arid conditions. Specific points such as the decline and disappearance of the floor component, or the dramatic increase in litter N as a percentage of phytomass N along the climatic gradient may provide valuable insights into operative processes, but the fact remains that this level of study is one of budgeting at a point in time--an essentially static description of minerals in plant communities, together with a minor concession to function as evidenced by the rather coarse criterion of annual turnover in litter.

It is important to have such information simply to provide a context for further work of a more detailed nature. Also, the initial delimitation will always pose new questions and show where further effort might best be directed. Nonetheless, the framework is a limited one, not just because of the way in which it obscures those driving functions whose integrated and fluctuating activities generate the annual mineral throughput, but because it is comprised of only one ecosystem compartment--the production component. Important as this may be, it is intrinsically impossible to arrive at an understanding of overall community function with respect to mineral cycling from its analysis alone and we must move to include other segments of the totality of community physiology if such understanding is our ultimate aim. Accordingly, at the second level, we can ask of the soil the same kinds of questions which were directed at phytomass.

The soil reserve

In the same way that measurement of minerals in standing crop and litter is a reasonable starting point for analysis of environmental influences on mineral pool sizes, so collection of chemical analyses is an appropriate beginning for work aimed at a descriptive statement of soil pools at a nonfunctional level.

Like any ecosystem property, total reserve of soil minerals is conditioned by interaction of the five major state factors (Jenny 1941; Major 1951; Crocker 1952). Of these, climate is generally accorded prime significance with respect to most characteristics, yet its importance can be locally modified to a considerable degree by topography, e.g., in the examples from an arid area given by Klemmedson (1964), or by parent material across quite a range of climate as shown by Hallsworth and others (1952). To illustrate the general nature of these controls on mineral capital it is sufficient to take the examples of N and P; both are of central biological significance, and each enters the ecosystem from a different point. In the case of N the origin is overwhelmingly atmospheric, whereas for P it is the soil's parent body which provides virtually the entire potential input.

Table 1.--*Biomass, annual litter fall and turnover of ash elements and nitrogen in some major vegetation types*[1]

Vegetation	Shrub tundra	Southern taiga pine forests	Beech forests	Meadow steppe	Semishrub desert	Solonchak desert vegetation	Takyr algal communities	Tropical rain forest
Mineral elements in plant biomass (g./m.^{2})	90	188	420	118	18	14	0.65	1,108
Mineral elements in litter fall (g./m.^{2})	11	5.8	35	68	5.9	8.4	.65	154
Mineral elements on floor of community (g./m.^{2})	420	173	100	80	--	--	--	18
Principal mineral elements in litter fall	N,(K,Mn)	N,Ca,K	Ca,N,Si (Al)	Si,Na,Ca (K)	N,Ca,K (Na,Cl)	Cl,Na,N (S,Mg)	N,Si,Cl (Ca)	Si,N,Ca,(Al, Fe,S,Mn)
Mean N concentration in litter (%)	2.1	0.3	0.9	1.2	1.5	2.8	1.4	1.0
N in biomass (g./m.^{2})	48	66	161	27	6.1	3.1	.15	294
N returned in litter fall (g./m.^{2})	5.1	1.6	8.2	16	1.8	1.4	.15	26
N in litter fall as percent of biomass N	11	2	5	60	30	45	100	9

[1]Adapted from Rodin and Basilevich (1965).

Table 2.--*Mean values of annual return of mineral elements in litter fall for some major zonal and intrazonal plant communities*[1]

Type of plant community	Mineral elements in litter fall (g./m.^{2})								
	N	P	S	Ca	Mg	K	Na	Si	Cl
Shrub tundra	5.2	0.5	0.2	1.0	0.5	2.1	0.2	0.6	0.1
Southern taiga pine forest	1.6	.3	.4	1.5	.3	1.0	--	.3	--
Beech forest	8.3	.9	.4	10	1.3	3.5	.2	6.1	.1
Meadow steppe	13-16	.9-1.6	.5-.8	2.5-13	1.4-3.1	5.6-12	.2-1	17-24	.7-.9
Semishrub desert	1.4-1.8	.1	.1	1.4-2.2	.2	.3-.7	.6-.8	.2	.4
Desert Solonchak vegetation	.9-1.4	.05	.2-.3	.4-.9	.1-.4	.5-.7	1.4-2.7	.1-.5	1.6-3.3
Takyr algal communities	.15-.9	.05	.05-.1	.1-.2	.05	.1-.5	.05-.2	.05	.1-.3
Tropical rain forest	26	1.2-1.8	3.3	18-31	5.8-7.2	5.3-8.4	.6	77	.2

[1]Adapted from Rodin and Basilevich (1965).

Despite the power of climate as a control, variations in parent material can be the predominant influence in determination of local vegetation patterns even where leaching potential is relatively intense and might be expected to overwhelm compositional differences between contiguous rocks which could give rise to soils of differing mineral status. Thus clearcut examples of rock influences are evident in floristic contrasts between serpentine soils and adjacent types (Kruckeberg 1954). Similarly, parent material P differences are known to be responsible for vegetation patterning in the forests of Eastern Australia (Beadle 1962) and could be important in molding the Australian flora generally (Beadle 1966). When arid and semiarid areas are considered, however, it is usual to find the role of parent material expressed almost exclusively in terms of its influence on soil texture and water relations. The view seems to be that with low leaching potential the products of rock decay must remain and accumulate in the soil to such an extent that there is no likelihood of nutrient shortage and limitation of vegetation production resulting from rock characteristics. For example, there is the opinion expressed by Hilgard (1941) that the soils of dry regions should be a storehouse of minerals requiring only water to unlock their potential productivity. In similar fashion, the dramatic flushes of growth which occur sporadically in deserts seem to be taken as evidence of high, absolute fertility. On the other hand, Jackson (1957) has indicated that these soils are about as heterogeneous as those elsewhere and that in a world view there are few generalizations about them which stand close scrutiny. Certainly they are sufficiently variable in mineral status for plant deficiencies other than N to occur, and for vegetation patterning to reflect parent material (e.g., Abdl-Salam and Sabet 1967; Roach 1955; Salisbury 1954; Winkworth 1964).

As in wet climates, then, chemical differences between parent materials can give rise to differences in local and regional site nutrient reserves such that the basic productivity set by climate can be curtailed. The position with respect to P is particularly interesting, especially when the possibility exists that its concentration may influence degree of N accumulation through limitation of biological fixation mechanisms (Walker 1962; Jackson 1962), and that deficiency can retard transformation of N from the organic to the inorganic pool (Cowling 1969).

Excepting small inputs which may derive from particulate atmospheric fallout, P capital of any natural ecosystem comes from the soil's parent body. These materials vary enormously in P content (Joplin 1963, 1965) and soils likewise (10 to 5,000 µg./g. includes the majority) with the pattern of distribution of soil P status reflecting the rock pattern which is not correlated with climate. Therefore, we might expect to find the average levels of soil P much the same in all arid zones if these areas contain roughly equivalent proportions of each class of rock. In like manner, as P compounds in soils are highly resistant to depletion by leaching, we might also expect mean values for arid and humid soils to be much the same. These expectations do in fact seem to hold, but there is a noteworthy departure in the Australian case (Jackson 1957). Thus the data of table 3, adapted from Charley and Cowling (1968), show P levels of Australian arid-zone soils to be much lower than the average for humid zones and lower overall than in equivalent climatic situations overseas. Stephens (1951), Wild (1958), and Beadle (1962) have examined this preponderance of low concentrations and in each case the explanation offered has had to do with polygenesis and the fact that many soils of Australia reflect the impress of past climatic regimes when P depletion could have taken place. No doubt similar differences of a more localized nature could be discovered in other arid lands, and more detailed examination would probably show related trends for other essential elements. Undoubtedly parent material does exercise a powerful influence on ecosystem mineral status in dry regions, yet the extent to which this is reflected in productivity will depend in the main on biological demand which is principally a matter of moisture availability.

Few data are available on soil P depth function for arid-zone communities whose phytomass nutrient contents have been determined. In consequence, much of the plant information cannot be interpreted in terms of total site capital and the proportions

Table 3.--*Frequency distributions of phosphorus concentration in soil samples from arid regions, and comparison of mean levels in some arid and humid regions of the world*[1]

Phosphorus content	Australian arid	Other arid	Soils	Samples	Mean phosphorus content
μg./g.	-Percent-				μg./g.
0-100	24	7	U.S. arid	573	700
100-250	39	6	Aust. arid	70	240
250-500	30	14	Other arid	70	710
500-1,000	7	54	Aust. humid	208	620
>1,000	0	19	Other humid	1,270	730
Mean P (μg./g.)	240	710			

[1]Adapted from Charley and Cowling (1968).

held in the separate system compartments. Nevertheless, an approximate picture of range of gross soil contents (table 4) has been calculated for a number of arid zone sites in order to illustrate the significance of soil reserves in relation to those of plant material. These data are themselves hard to interpret unless the effective "biological" volume of the soils is known. Otherwise a small increase in the depth used in calculation of gross quantity can greatly overestimate the total pool which is potentially functional. Realistic estimates of these pools are always difficult to obtain because they require information about "labile" and "non-labile" fractions of the soil pool.

In the case of N the most important source is the atmosphere and the extent to which there is transfer from this supply is mainly a question of climate (Jenny 1928, 1930, 1941). The origin and distribution of N in soils has been reviewed recently by Stevenson (1965); thus it is sufficient here to mention briefly some of the work relating directly to arid-zone soils.

Table 4.--*Organic and total phosphorus capital and distribution in a selection of profiles from arid regions of the U.S.A. and Australia*

Soil	U.S.A.[1]			Australia				Overall means
	1	2	3	1	2	3	4	
Total P, 0-50 cm. (g./m.^{2})	343	575	581	252	132	131	43	294
Org. P, 0-50 cm. (g./m.^{2})	40	84	145	35	52	74	--	72
Org./Total (%)	12	15	25	14	39	57	--	27
Total P, 0-10/0-50 cm. (%)	27	22	26	13	19	18	14	20
Org. P, 0-10/0-50 cm. (%)	66	33	47	20	16	19	--	33

[1]Calculated from analytical data of Fuller and McGeorge (1951).

Limited amounts may accumulate in arid communities from organic and fixed ammonium N in parent material, especially shales and slates (Stevenson 1959). There will also be inputs from particulate fallout of an organic nature (Drover and Barrett-Lennard 1953), as inorganic N dissolved in rainwater (Eriksson 1952; Bobritakaya 1962), and perhaps through adsorption of ammonia from the air (Ingham 1950; Malo and Purvis 1964).

While each of these may on occasion be significant, biological fixation of N is undoubtedly of overriding importance. The *Rhizobium*-legume symbiosis is not easy to assess quantitatively but herbaceous species are certainly effective at times when climatic conditions are unusually favorable and dense populations develop. For woody species the position is less clear; many are known to nodulate freely in artificial culture and nodules may occur in the field (Beadle 1964; Wagle and Vlamis 1961), but the level of annual fixation is unknown and for some species may be quite small. Thus Garcia-Moya and McKell (1970) in a study of differences in soil N under leguminous and nonleguminous desert shrubs could find no evidence which would indicate that the former were responsible for upgrading N status.

Because intensity and duration of operation of the biological mechanisms responsible for N fixation are controlled by available soil moisture, N content of soils is strongly correlated with climate as illustrated by the U.S.S.R. data of table 5. All arid-zone soils are low in N, yet there is a substantial range of variation between and within separate regions (tables 5 and 6, Australian data) which must reflect the influence of certain soil texture and rainfall distribution differences on duration of available soil moisture.

In general, these measurements of total soil capital provide a much better perspective for studies of plant mineral content and the magnitude of annual turnover. They tell us something of the size of the mineral reserve which can take part in productive processes of the community, and they may also bring to light significant differences in mineral distribution between soils and plants of vegetation types representing contrasting environments. Apart from this, however, they do not add much to our

Table 5.--*Total capital and distribution of nitrogen in some major great soil groups of the U.S.S.R. and arid Australia*

Soil	Soil N (Tons/ha.)		0-20 cm./0-100 cm.
	0-20 cm.	*0-100 cm.*	*Percent*
U.S.S.R.[1]			
Podzolic (average)	3.2	6.6	48
Gray forest	6.0	12.0	50
Chernozem (deep)	11.3	35.8	32
Chernozem (southern)	6.3	17.0	37
Sierozem	3.8	11.8	32
AUSTRALIA			
Desert loams	2.4	5.1	47
Solonetz	2.2	4.1	54
Stony tableland	1.8	3.8	48

[1]Data from Tiurin and Kononova (1962).

Table 6.--*Nitrogen content frequency distributions for some soil samples from Australia and other arid regions*[1]

Soils	Samples	Total Nitrogen (%)						Mean N content
		<.01	.01-.03	.03-.05	.05-.10	.10-.50	>.50	
		-Percent of samples-						
Australia humid	138	0	1	4	19	70	6	0.22
Australia arid	77	4	22	23	41	10	0	.06
Overseas arid	38	0	16	29	18	37	0	.11

[1]From Charley and Cowling (1968).

understanding of mineral cycling because there is no indication at this level of study of how much of the soil pool is directly involved in those processes which exercise major control over vegetative production in the short term. It would be expected that continued repetition of the annual uptake-litter fall-decomposition cycle would result in an increasingly complex distributional structure of minerals intimately associated with the soil's organic regime, and that this successional restructuring of the mineral pool would reflect something of the nutritional organization of the community as a whole. But, as in the case of phytomass mineral pools, soil mineral reserves are calculated from concentration averages which obscure anything of value concerning spatial variability which could indicate the proportion of total capital involved in short-term physiological activity of the community. Accordingly, if simple chemical analysis of the soil body is to reveal anything reflecting function in mineral cycling then it must be pitched at a level of detail well beyond that which is adequate for establishing the size of the substrate mineral reservoir; it must aim at discovering the "shape" of the reservoir.

Structural organization of the soil mineral pool

All soils show some degree of accumulation of nutrient and other elements towards the surface though the arid environment accentuates this tendency by confining most biological activity to the first few inches of the profile. These gradients are best developed in the case of N and organic matter, but elements such as P behave in similar fashion even though they may not be as clear because local concentration is seen against the background of a relatively large inorganic pool. In general it seems that biologically induced vertical gradients become sharper with increasing aridity (Charley and Cowling 1968). Further, if comparisons are made between soils developed from parent materials of differing composition, those of the lower end of the fertility spectrum show greater proportionate accumulation in topsoil.

Most biologically important minerals of the soil compartment are distributed along concentration gradients simply because plants are the basic physiological units involved in movement and these are discrete. Root systems explore to some depth and well beyond the canopy projection, yet litter fall tends to be localized beneath the foliage. Because they are mobile, some minerals may be moved by percolating water and other agencies away from their point of deposition once they are released from the decomposing organic regime. In the main, however, return is overwhelmed by rate of local concentration so that patterns resulting from litter fall accentuate as the ecosystem matures. In fact, once formed, these patterns can remain as evidence of establishment sites long after the causal vegetation is removed; a good example of pattern longevity common in Western New South Wales is the relatively prolific ephemeral production which occurs in haloes about old stumps of the legume *Acacia aneura* as a result of increased soil N status here.

Under closed-canopy conditions minerals of litter fall tend to be uniformly distributed over the floor of the community and only vertical soil gradients develop to any extent. Then, as density decreases, and individual perennials space out, the soil mineral pattern resolves into lateral gradients between volumes of depletion and accumulation. If growth of annuals is profuse on soil surface between perennial units a degree of backflow may occur, but this is probably slight under normal circumstances.

Arid-zone shrub communities have provided some of the most striking examples of anisotropy in soil mineral distribution. So much would be expected from the way such shrubs tend to be regularly spaced over the surface in consequence of limited moisture. But as far as organic N is concerned, clarity of pattern is enhanced because total N status is low.

Pattern definition is influenced by many factors, several of the most significant being mineral selectivity differences between species, shrub habit, and the nature of rainfall distribution. In the first case, plants such as the facultative halophyte *Atriplex vesicaria* can sieve from their rooting volume large quantities of soluble salts such as chlorides of Na and K even though these may be at quite low concentration in the medium (Wood 1925; Beadle and others 1957). Soil under these shrubs can thus develop quite different ion proportions to the general surround and differing also from the salt complex beneath associated species with other selectivity characteristics (Fireman and Haywood 1952; Rickard 1965).

Shrub habit may be important where it affects retention of litter at the site of deposition. For example, two ecotypes of *A. vesicaria* differ in that one is upright and sparse, the other hemispherical and intricately branched right to the soil surface. Litter fall in the latter is therefore retained better against wind dispersal and the integrity of the mineral micropattern maintained. Similarly, there are contrasts in the genus *Kochia*, and no doubt many other examples could be described.

Rainfall characteristics may also be influential in that they determine the bulk and regularity of ephemeral production between shrubs and the extent to which mineral accumulations under shrubs are likely to be tapped and redistributed for a time to a spatially separate mineral subpool.

Micropatterns of mineral distribution

Few detailed studies of mineral mosaics have been made in arid-zone shrub communities, yet pronounced localization of concentration is evident in each case reported. Thus Fireman and Haywood (1952), Roberts (1950), and Rickard (1965) describe instances of sharp increases in pH, exchangeable Na and K beneath shrubs as a result of litter deposition, and considerable differences between species in this regard. Similarly, Garcia-Moya and McKell (1970) and Charley and West (unpublished) have found equally significant accumulations of N beneath shrub canopies. However, as Charley (1959) and Charley and McGarity (1964) have shown, not all accumulations are towards growing shrubs but may take place in soil between individual bushes or clumps of bushes. In these instances unusual accumulations of chloride and nitrate have been found to be a general feature of perennial saltbush communities growing on fine-textured saline soils of the Australian arid zone. But these concentrations of soluble salts are not stabilized unless the surface between plant aggregations is highly impermeable and therefore not subject to leaching. Buildup here results from lateral and vertical transport of ions in diffusing soil solution and not through litter deposition. In most cases chlorides have reached such high levels that no plants establish unless there is a succession of heavy falls of rain to reduce the salt content of the soil to tolerable levels. Even then it is a short-lived change, for a return to more normal rainfall sees the reestablishment of the salt mosaics in the same place and obliteration of plant growth there.

Detailed chemical analyses such as those mentioned above are adequate for characterization of the kinds and degrees of mineral capital redistribution which results from mineral cycling. But from the point of view of community nutrition and its relationship to plant growth, it is important to discover whether or not these accumulations of minerals created by shrubs are likely to enhance or lower production per unit of land surface. For example, there would seem to be no immediate benefit in buildup of large salt loads beneath halophytic species other than a possible lessening of competition for moisture from ephemeral growth of lower salt tolerance; such progressive change may in fact be accompanied by declining productivity from establishment sites through lowered water-use efficiency and slowing of the microbial activity responsible for liberation of essential elements from organic matter. On the other hand, local increase in organic N can only be interpreted as an advantage, especially when mean soil N status of the community is low, because it implies a direct raising of the N-supplying potential of the plants' immediate substrate surround.

An important question which remains is the rate at which pockets of mineral accumulation develop and whether in fact they reach an equilibrium within the lifespan of the causal individual or go on intensifying up to the time of death. For exchangeable Na the rate of accumulation is apparently quite rapid according to the shrub-diameter greasewood sequence given by Fireman and Haywood (1952), but apart from this example there is little to go on.

Soil fertility patterns in shrub communities

The relationship between plant-induced micromosaics of mineral distribution and fertility status of the soil can be established by the use of a number of simple biological measures of nutrient supply rate. These include direct growth assessments of relative fertility and determination of organic N mineralization rate. Such methods are quite commonly applied in agricultural areas but they have only recently been tried on arid-zone soils.

Depth functions of relative fertility as measured by these techniques (Cowling 1969) have clearly established that nutrition of perennial saltbush communities in New South Wales is closely tied to availability of nutrients in the top 5-10 cm. of the profile as soil below this supports very little plant growth. Relative dry weight production of saltbush plants grown on samples taken from increasing depth in a given profile, and from eroded and noneroded profiles (table 7), shows abrupt decline in

Table 7.--*Fertility decline with depth in saltbush soils as shown by plant growth and mineral nitrogen production in samples from different horizons*[1]

Sample depth (cm.)	Plant production		Sample depth (cm.)	Mineral N production		
	Eroded soil	Normal soil (1)		Soil 1	Soil 2	Soil 3
	Mg. dry weight			*µg./g. dry weight*		
0 - 7.5	377	595	0 - 2.5	235	284	430
7.5-15.0	195	270	2.5- 5.0	151	113	336
15.0-22.5	34	214	5.0-10.0	84	86	261
22.5-37.5	27	46	10.0-15.0	54	62	30
			15.0-22.5	47	43	24

[1]Adapted from Charley and Cowling (1968).

short-term nutrient supplying potential below the immediate surface (Charley and Cowling 1968). In similar fashion, nitrification determinations in the same soils indicate a close correlation between inorganic N production potential and plant productivity (table 7) and emphasize the point that community nutrition is determined in the main by chemical status and biological activity of surface soil. Subsoil, it would seem, plays a minor nutritional role in dry environments, except perhaps in the long term where it could serve as a reservoir of elements such as P which are gradually being brought into the superficial organic regime. Otherwise, the chief contribution of soil at depth is probably as a reservoir of moisture.

Lateral variations in chemical status brought about by localization of litter fall beneath shrubs are also known to reflect sharp gradients in labile N as measured by nitrification. Charley and West (unpublished), in an examination of the role played by shadscale bushes in creation of soil mineral mosaics, have established by aerobic incubation tests that mineral N supply potential is concentrated beneath the shrub canopy and decreases very rapidly downwards and outwards. Nitrate produced in a 2-week experimental period fell from 404 µg./g. in the top inch of soil beneath a bush to 95 µg./g. in the 1- to 2-inch interval, 33 µg./g. between 2 and 4 inches, and only 19 µg./g. in the 4- to 6-inch slice. Laterally, the decrease in the 0- to 1-inch layer was also sharp with values for nitrate at 404 µg./g. under the canopy, 240 µg./g. 8 inches out from the canopy edge, and 166 µg./g. at a distance of 18 inches from the edge. The latter point represented soil collected in bare space midway between adjacent shadscale bushes.

A further significant trend shown by these results is a greater proportionate increase in mineralization as total soil N content rises. It is known (Clark and Paul 1970) that the N pool of grassland soils consists of several fractions of differing reactivity; thus there is a component consisting of decomposing plant residues and associated biomass which turns over at least once every few years, a subpool of microbial metabolites and cell wall constituents that become stabilized in soil and have a half-life of 5 to 25 years, and a resistant fraction which is comprised of humic compounds ranging in age from 250 to 2,500 years. It is therefore possible that the shadscale data reflect a similar situation with most of the nitrate deriving from decomposition of the younger organic N residues which are concentrated in the immediate vicinity of litter deposition sites. If this is indeed the case, then it implies that the pockets of N accumulation which result from litter deposition beneath bushes are a development in the direction of more efficient utilization of N than would be the case where the total reserve spread evenly through the soil body.

Soil processes and mineral cycling

So far all comment has been concerned with essentially static descriptions of minerals in shrub communities--determinants of total reserves, partitioning of this capital between soil and plant compartments, and the ways in which relatively small and isolated perennials bring about qualitative and quantitative reorganizations of the total element pool during maturation of the ecosystem. Separately or in combination, neither biomass nor soil-compartment mineral contents can tell us much about the role of minerals in the ecosystem as they are gross quantities with little sensitivity for reflecting function. As shown by preceding sections, more detailed analysis of the structure of separate pools will, however, reveal something of the organization of the system and the role of plants in the restructuring of mineral reserves within their sphere of influence. Previous examples also show that a closer focus on mineral distribution may be sufficient to indicate where important processes such as N mineralization are concentrated. There is no questioning the essentiality of this kind of background information, for just as gross morphology and anatomy describe the framework of physiological activity in plants, so size and configuration of the ecosystem mineral reserve provide a reference for the study of process in cycling. Nonetheless, there is a limit to the usefulness of these approaches.

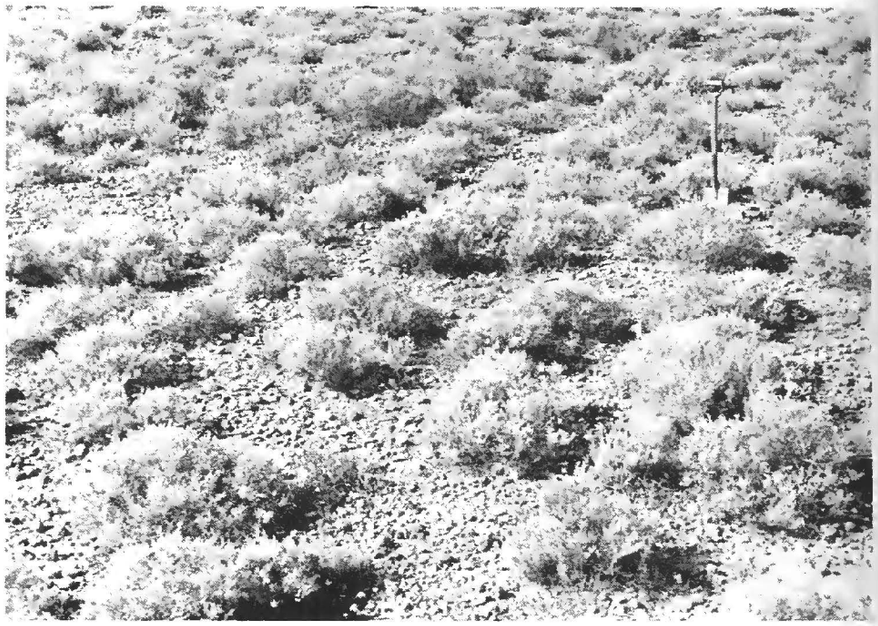

Figure 1.--Atriplex vesicaria *community growing on fine-textured saline soil, Broken Hill region.*

Perhaps a more profitable way to view mineral cycling is as a reflection of community nutrition, or as a matter of rates of supply in relation to potential demands. On this basis, it is the examination of mineral transfers through the various gates which link to form the mesh of community function which is most likely to show how the system works and where limitations of nutrient flux brought about by environmental fluctuations may influence productivity. In effect, it reduces to analysis of individual processes within localized mineral pools of the soil body.

It could be argued that mineral cycling studies which concern themselves with turnover in litter on an annual basis are looking at the problem from the wrong end. Such measurements will indicate throughput, but the important nutritional activities are over by this stage; the minerals of litter have served their function and are waste materials being returned for processing in the transformation-decomposition machinery from whence they will emerge in inorganic form to determine once again by their level of supply and fluctuation in time the adequacy of fueling of the primary production compartment. If the gross level of a nutritionally important mineral is low, then reprocessing of this element must be rapid if deficiency in relation to demand is to be avoided. If, on the other hand, the total is high, a lesser level of process activity may serve to meet requirement and avoid curtailment of production. In sum, then, it seems much more likely that an understanding of mineral regulation in the productive display of an ecosystem will emerge from inquiry into activity patterns in the physiological milieu of the soil than it will from even the most exhaustive analysis of the aboveground compartment of the system.

Some artificial or induced ecosystems have been approached in this way, notably certain agricultural, pastoral, and forest monocultures of temperate regions. In dry areas, on the other hand, the sum total of work is limited and the individual studies largely disconnected. Nevertheless, the case for N has been explored to some extent and is sufficiently well understood to serve as illustration of the importance of soil biology in community nutrition and mineral cycling. Phosphorus could be used but it has not been studied to any extent in shrub communities of arid lands, nor is it likely to be as significant in the control of plant production as N which is the nutrient most commonly in short supply where rainfall is low.

The specific example chosen for analysis is an *Atriplex vesicaria* ecosystem of saline soils in Western New South Wales. This vegetation type (fig. 1) is common in the southern part of the Australian arid zone and its N economy is reasonably well understood at the quantitative structural and functional levels. Each of these separate analytical approaches will be briefly considered.

Nitrogen economy of a perennial saltbush ecosystem

Nitrogen Capital

Table 8, adapted from Charley and Cowling (1968), gives the distribution of organic matter, nitrogen, and phosphorus within and between separate compartments of the saltbush community mentioned above. While these data show that the quantities tied up in phytomass and cycled in litter are an insignificant proportion of the total, they nevertheless demonstrate that the turnover time in standing crop is quite short with a little more than one-third of this amount going through the deposition-decomposition pathway each year. Further, total weight of litter fall for the year was greater than the weight of leaf held in the community when it was in good condition, and this evidence of rapid breakdown is supported by the negligible litter mat. It should be noted, too, that litter has a lower nitrogen and phosphorus content than fresh leaf indicating withdrawal into the stem prior to abscission.

Table 8.--*Distribution of organic matter, nitrogen and phosphorus in soil and plant material of an* Atriplex vesicaria *community*[1]

Compartment	Organic matter	Total nitrogen		Total phosphorus
	------ *G./m.*[2] ------			
Above ground:				
Leaf	82.5	1.6		0.07
Wood	140	0.8		.03
Litter	14.8	.06		--
Total	237.3	2.46		0.10
Below ground:				
Roots[2]	91	.6		.03
Soil (0-45 cm.)	3,704	265	108	
Total	3,795	265.6	108	.03
Litter fall (1 yr.):				
Leaf	68.4	.43		.03
Fruit	36.1	.45		.04
Wood	4.9	.01		--
Total	109.4	.89		.07
Above/below (%)	6	1		.1
Turnover/above (%)	46	36	65	

[1]Adapted from Charley and Cowling (1968).
[2]Estimates.

Shrub Growth and Localization of N Capital

In a functional sense, this saltbush community is an aggregation of generally discrete basic units consisting of a single saltbush shrub together with a small area of surrounding land surface. This unit functional cell may not be able to exist in isolation from its neighbors. Nonetheless, within its volume should be found a full display of the processes which combine to form the mineral throughput pathway. In consequence, analysis of the structure and the function of this basic physiological cell should reveal the nature and activity of all static and dynamic aspects of mineral cycling and nutrition contained in the ecosystem as a whole. The structure of such a microcosm has been analyzed and its relevant characteristics are set out in figure 2.

For those who incline to extrapolation, it should be mentioned that the chosen unit cell is not an average one in a quantitative sense; in order to ensure a clearcut illustrative case of the shrub effect in localization of minerals, a large (50 cm. diam.), vigorous and geometrically uniform saltbush plant was selected for study in the hope that N distribution in its soil volume would be reasonably symmetrical. Two further points in explanation--the area of surface surround is somewhat larger than the share of the bush in question, and the cell depth of 50 cm. was used for calculation purposes as this was the level at which significant root development appeared to cut out. The N fractionation given was calculated from analyses of standing crop, a 1-year litter-fall collection, and nine soil profiles taken along a 2.5-m. transect through the middle of the establishment site. Distribution of soil N is shown in figure 3.

On the basis of total cell content, phytomass N represents only 0.7 percent of the whole and consists mainly of root N, a finding in agreement with the data of Rodin and Basilevich (1965). The individual soil analyses show that the shrub has brought

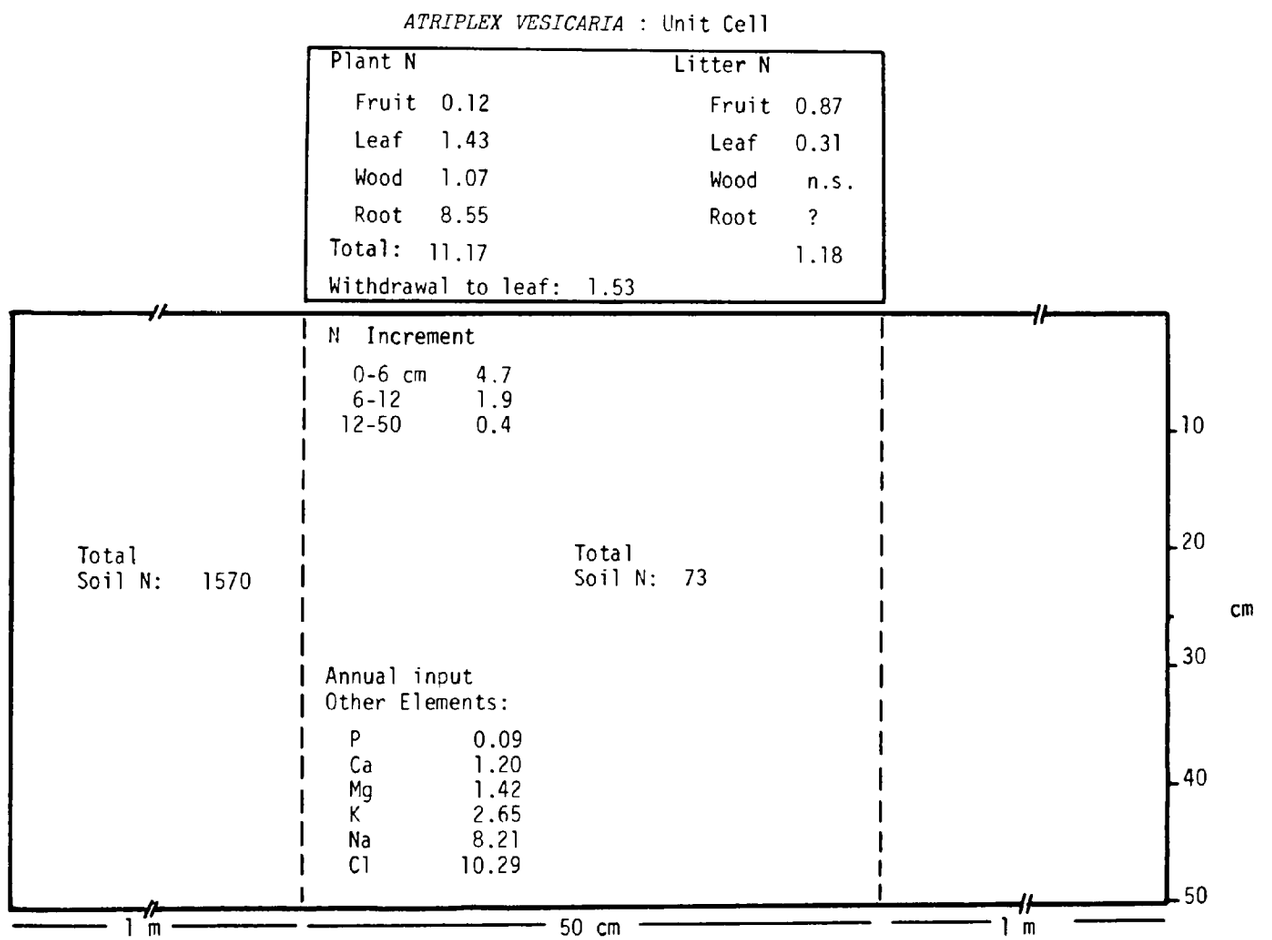

Figure 2.--Distribution and turnover of N and litter input of other elements in a single bush unit cell of an Atriplex vesicaria *community, Broken Hill region.*

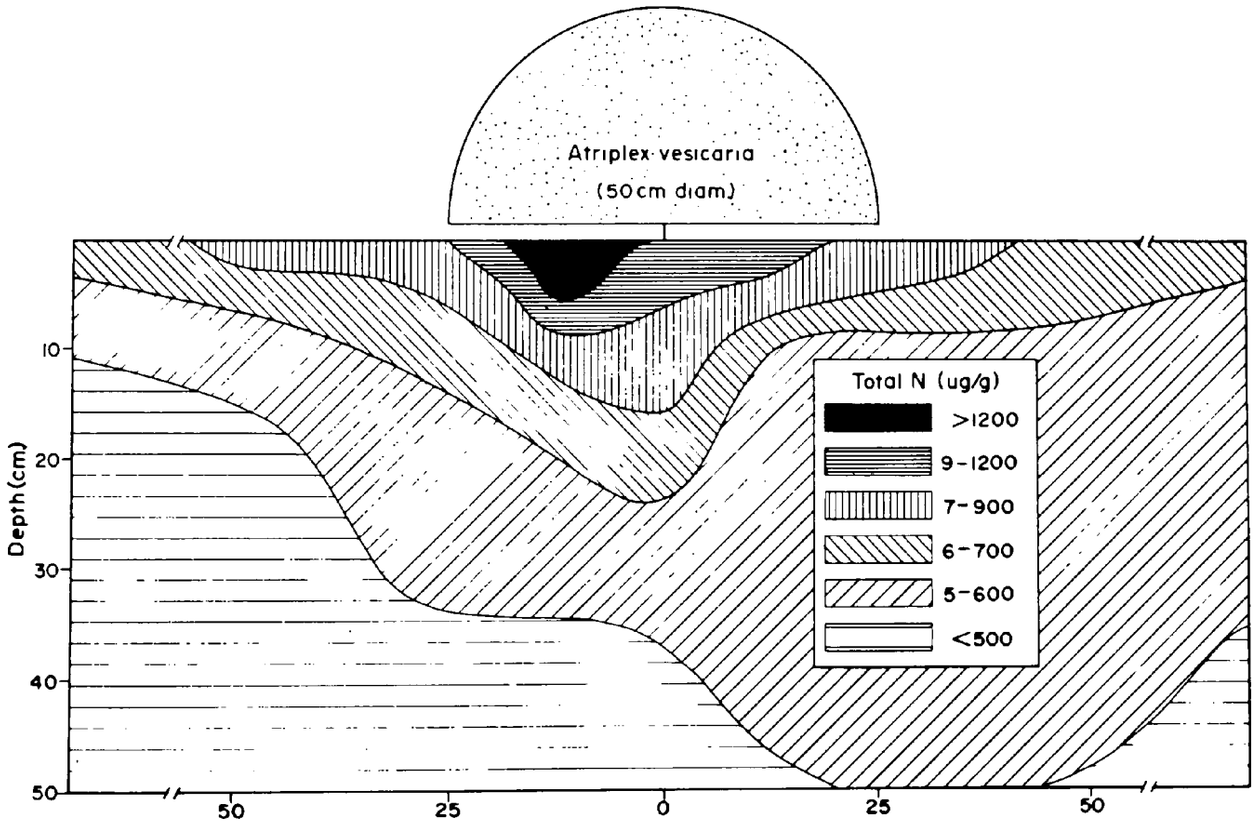

Figure 3.--Distribution of N in the soil beneath a single Atriplex vesicaria *bush showing surface concentration resulting from litter fall.*

about a general lowering of N concentration in its surroundings and that this uptake has accumulated immediately beneath the canopy. A total of approximately 7 g. of the element has been added to the soil beneath the foliage, most of it in the top 6 cm. of the profile. Although a very small proportion of total N in the unit cell, this increment represents 10 percent of the below-canopy soil content. If only the top 12 cm. of the central soil column is considered, N accumulated here as a result of shrub growth comprises 27 percent of the total or 38 percent increase in concentration. For the first 6 cm. of the central core the buildup is 4.7 g., a 59 percent increase on the average, which would obtain if all N in the unit cell were uniformly distributed throughout its volume.

The total shrub effect on N distribution is approximated by all plant N above and below ground plus that increment in the top 12 cm. of the soil under the foliage. This amounts to 19 g. or 22 percent of all N above and below the canopy spread. The same accumulation represents 46 percent of all N held in the bush and the 0-12 cm. slice beneath the bush, a highly significant amount when it is considered that probably most N transformations and movements take place in this subvolume of the cell. It is impossible to say with any certainty how much of this localized concentration derives from fixation in the microsite and how much can be attributed to withdrawal from the immediate surroundings, but the indications are that it is mainly a question of redistribution within the unit cell.

Annual Turnover in Litter

Nitrogen in litter fall is a very small part (0.07 percent) of total cell capital yet comprises 10.6 percent of all plant N. If return in root residues had been measured the percentage would undoubtedly increase substantially as observations in

root-growth boxes have shown that a high proportion of fine roots dies off each time the soil goes through a drying cycle. Dieback must occur quite frequently in the field where several such drying cycles can be expected each year.

Analyses of live and freshly fallen leaves and fruits of *Atriplex vesicaria* point to significant movement of N to woody tissue prior to abscission. In the present case this withdrawal amounts to more N than was actually returned in surface litter. It is well known that leaf N is highly mobile in plants, particularly under conditions of water stress, but the ecological significance of its return to the stem is not clear. Assuming that it remains mobile and available for reutilization when growth resumes, the 1.53 g. previously withheld from the decomposition pool of the unit cell could make a sizable contribution to new leaf development. In fact, in this instance, the amount withdrawn is equal to the total quantity of leaf and fruit N held at the time the shrub was harvested.

Annual deposition of other elements beneath the shrub must also be important in modification of the microsite as it represents an input of about 120 g./m.^{2} of this kind of surface. Phosphorus is too small to be of much significance, but Ca and Mg return is sufficiently intense to play an important part in stabilization of soil colloids against the dispersive effects of the heavy Na input.

Clay content of these soils averages about 30 percent in the surface and the cation exchange capacity about 40 m.-equiv./100 g. of clay. Thus an Na deposition of 8 g./annum would saturate the exchange complex of all soil beneath the bush to a depth of 12 cm. in 9 years if all was absorbed. Obviously this will not occur in the presence of substantial quantities of the other cations, but there is little doubt that analysis would show a high percentage saturation with this ion similar to the greasewood example described by Fireman and Haywood (1952). The heavy chloride input is not as important as it may seem, for relative accumulation beneath shrubs is generally only moderate. Unlike the cations, chloride tends to move downward and laterally in the soil to accumulate below bare surface between individual plants if they are reasonably spaced.

Litter Decomposition

At the time litter collection was commenced, plant residues were negligible indicating either that the previous year's fall had been slight or that decomposition of saltbush material is rapid. The only available decomposition study for *A. vesicaria* leaf material (Beadle, personal communication) supports the general conclusion with field observations; it demonstrates rapid loss of dry weight and decrease in organic N content. Samples of litter were arranged on screens in contact with columns of sand sunk into the soil and after 1 year of exposure to field conditions the residue was weighed and analyzed for N. The results show a 35 percent dry weight reduction and the loss of 39 percent of the original N content after five separate falls of rain totaling 69 mm. Mean annual rainfall for the area is approximately 200 mm.; thus all surface organic matter might be expected to disappear in 1 year or a little more if allowance is made for its increasing resistance to decomposition as breakdown proceeds.

Factors Affecting Nitrogen Mineralization

Mineralization of organic N is qualitatively very similar in all climates except that the low-pH inhibition of ammonia-oxidizing organisms that is common in humid regions is unlikely to occur in dry environments, and the accumulation of nitrite found in highly alkaline soils of arid areas as a result of *Nitrobacter* inhibition (Fraps and Sturges 1932; Martin and others 1942; Chapman and Liebig 1952) must be rare where rainfall is sufficient to through-leach the profile. Quantitatively, however, differences would be expected because of contrasting temperature and moisture regimes.

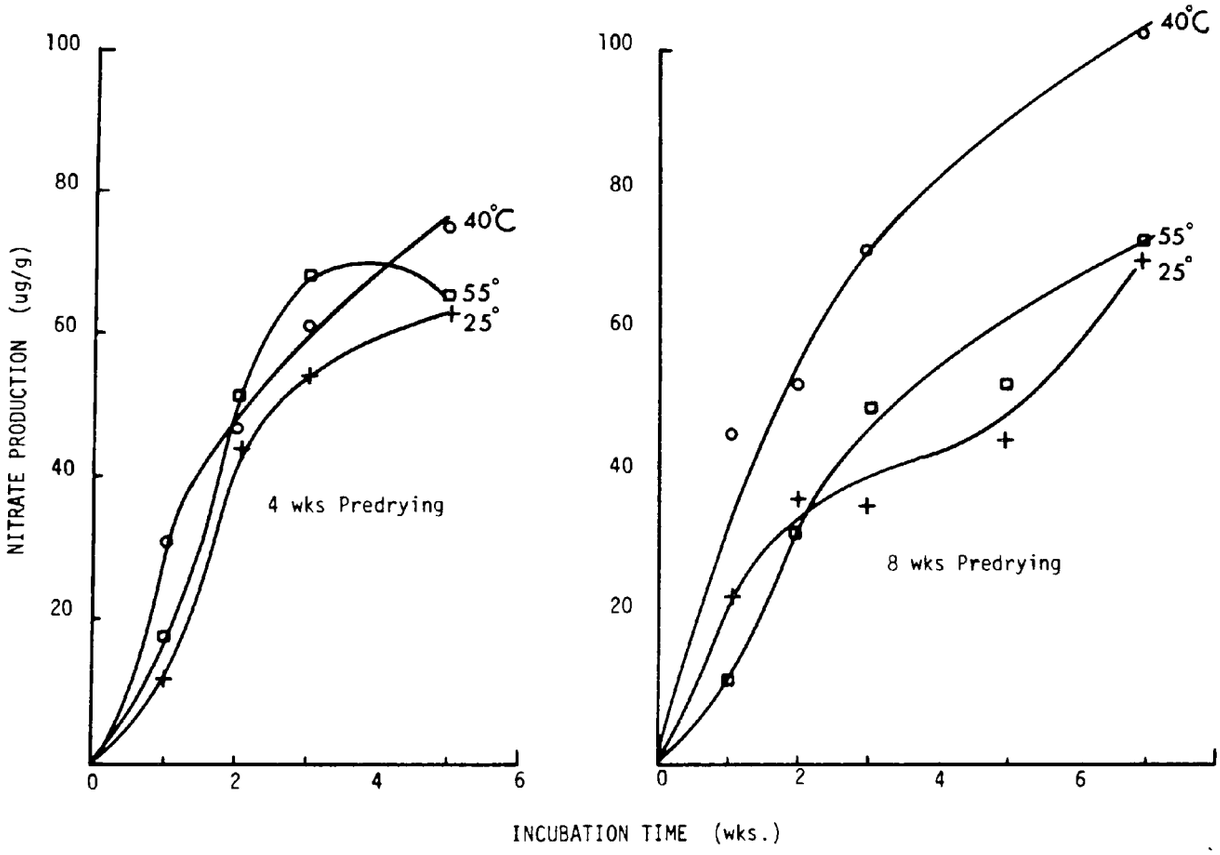

Figure 4.--Nitrate production in saltbush soil incubated at 35° C. following dry pretreatment for different times and temperatures.

Temperature.--Nitrosomonas, Nitorsococcus, and *Nitrobacter,* the principal agents of the ammonia-nitrite-nitrate oxidation, are known to occur in some of the most inhospitable regions of the arid world (Sims and Collins 1960). These organisms have evolved considerable heat tolerance and in arid areas may operate most effectively at temperatures well above the average.

Water potential.--Decomposition of organic matter and microbiological transformations of soil organic N to inorganic form are both markedly influenced by soil water potential (Ekpete and Cornfield 1965; Wetselaar 1968). At the higher end of the moisture range these decompositions are limited by restricted oxygen supply due to moderate or complete filling of the pore space diffusion pathway (Rixon and Bridge 1968). At low water contents lowered biological activity is principally a question of moisture stress, but there are interesting differences in response between ammonification and nitrification.

Soil drying.--The combined effects of temperature and soil drying are particularly interesting and significant in the context of an arid regime. Birch (1959, 1960) and many others subsequently have shown that most soils of tropical and temperate regions undergo accelerated mineralization of organic matter when wetted from an air-dry state. It is also apparent that the longer a soil remains dry the greater the decomposition activity following wetting up. This mineralization effect has been shown to apply in saltbush soils of Western New South Wales also and to be influenced by the temperature of the dry phase (fig. 4).

After 40° C. predrying, nitrification is faster than for both lower and higher temperatures during drying. Prolongation of the dry phase accentuates this temperature effect up to 40° C., but beyond that there appears to be an increasing lag due, perhaps, to a reduction in the population of nitrifiers.

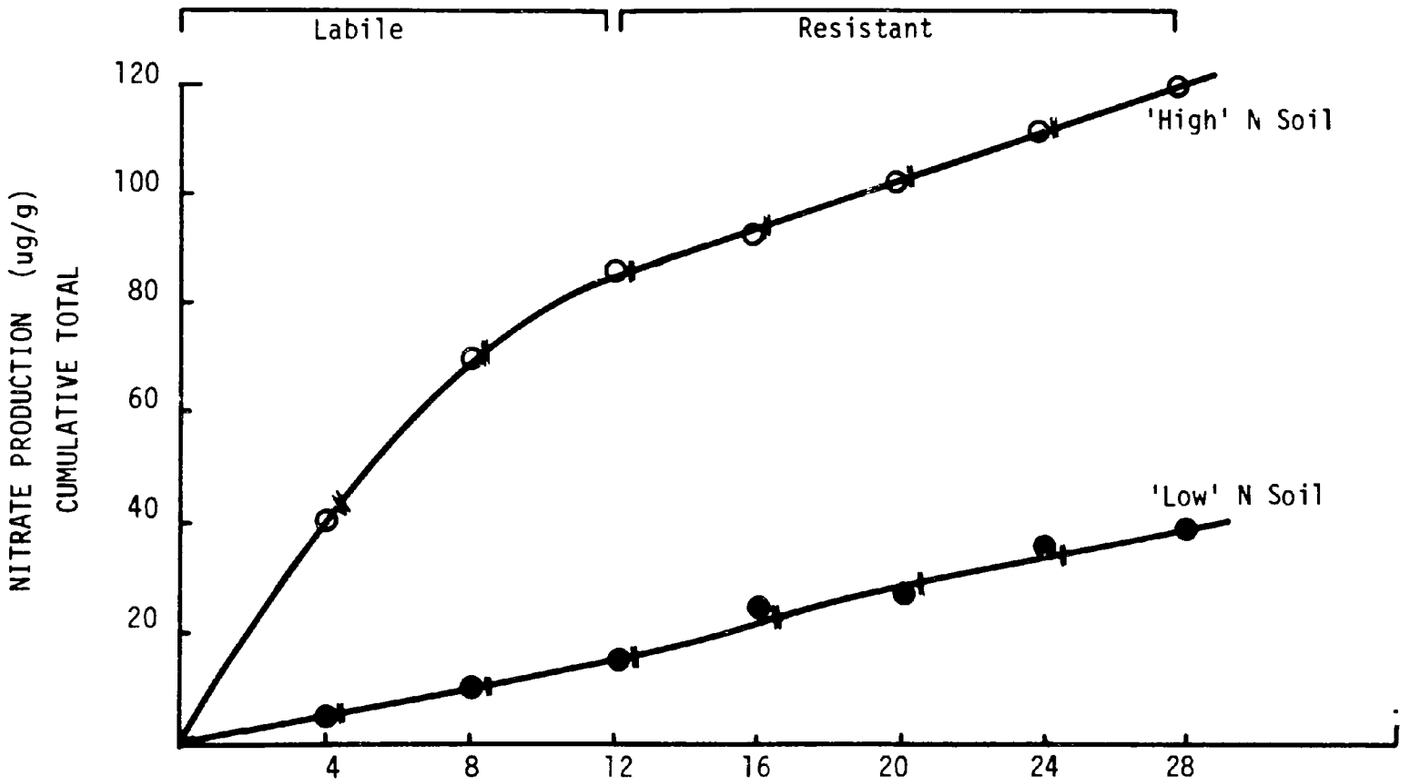

Figure 5.--Nitrification in soils of contrasting N status subjected to a cyclic treatment of 2 weeks of wetting followed by 2 weeks air drying; temperature of dry and moist phases 35° C.

The burst of respiratory activity that follows drying and remoistening has variously been attributed to partial sterilization of the soil population of microorganisms, physiological youth of surviving organisms, free enzymes in the soil, destruction of inhibitors, and physical alterations of organic residues which render them more susceptible to decomposition. For a given drying period the amount of nitrogen mineralized is a function of the humus content of the soil; less nitrate results from treatment of soils low in organic nitrogen and carbon (Birch 1960). Further mineralization can be stimulated repeatedly by drying and wetting. Thus Birch and Friend (1961) working with a soil of high humus content found after 204 such cycles that 100 percent of organic P, 63.5 percent of organic C, and 46.4 percent of organic N had been mineralized.

The cumulative totals for nitrate production (fig. 5) show quite different trends depending on total N content; there is no evidence of a flush of activity in the low-N soil. The difference in behavior may be attributed to relative proportions of labile and nonlabile N in each sample. Clearly, however, the magnitude of the drying effect declines as the pool of organic N is eroded by biological activity. Nevertheless, drying at moderate temperatures does continue to promote mineralization even after the most reactive fractions have been attacked. Thus, extrapolation of the linear sections of the curves to a total moist time of 28 weeks gives values of 177 µg./g. and 74 µg./g for high- and low-N soils, respectively, whereas parallel samples, which remained moist for the duration of the 7-cycle treatment sequence, produced 159 µg./g. and 31 µg./g. In all, the 7-cycle treatment sequence resulted in mineralization of 13 percent of organic N in the high-N soil and 7 percent in the other.

Rainfall Characteristics

The importance of rate of microbiological response to wetting of the soil becomes apparent when rainfall characteristics of the environment are studied. A frequency distribution of rainfall size classes at Broken Hill, Australia, for a recent 10-year

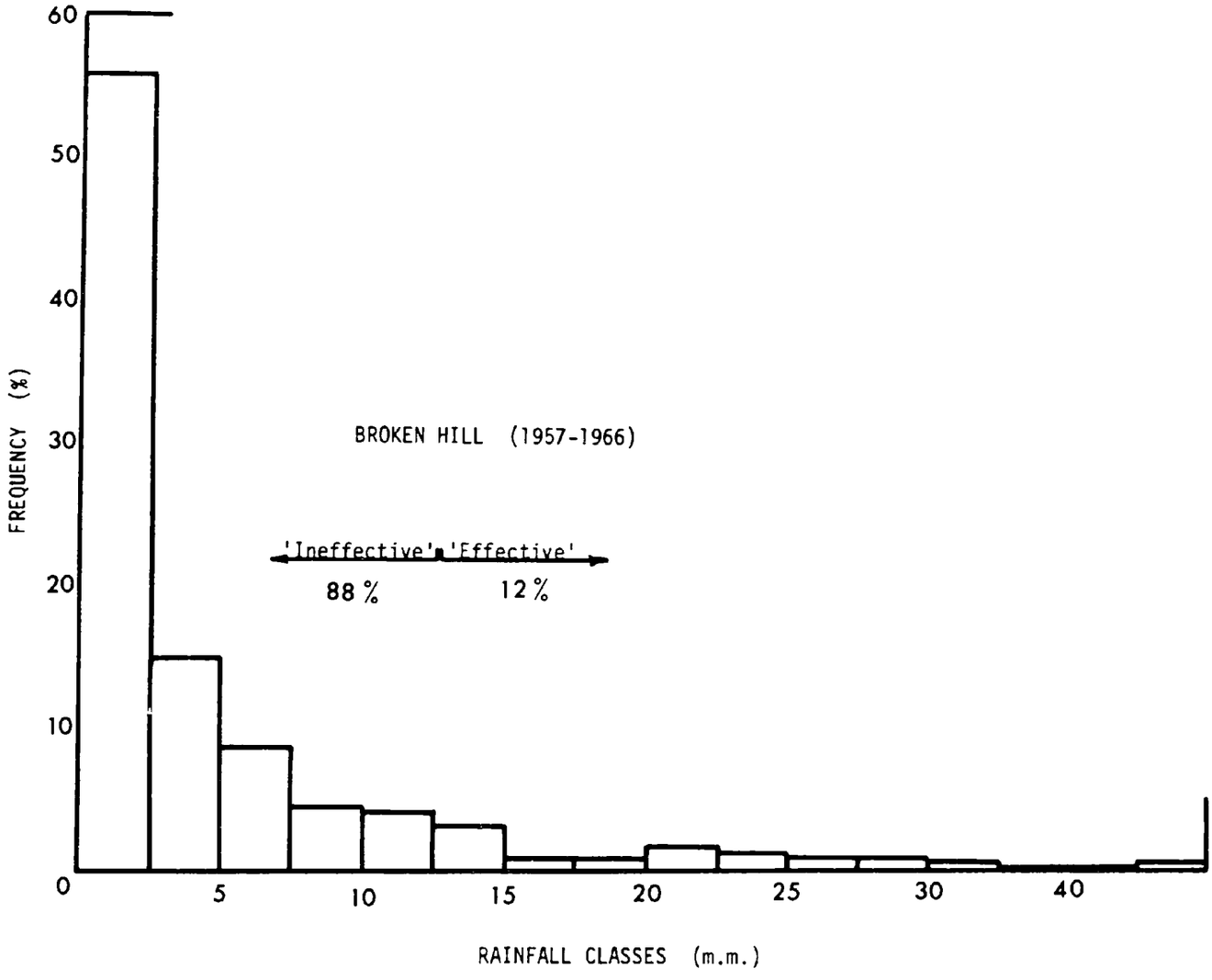

Figure 6.--Frequency distribution of rainstorms and precipitation totals typical of semiarid Western New South Wales.

period (fig. 6) reveals that the great majority of showers recorded in this area penetrate less than 5 mm. and that more than half the total number of falls can be expected in the 2.5-mm. category. Add to this poor quantitative pattern a highly erratic temporal distribution, and it becomes obvious that effectiveness in terms of plant production must be very low.

Most showers wet only the first few centimeters of soil, with the result that evaporation dissipates moisture before the vegetation can respond, particularly if superficial roots have been in dry soil for any length of time. According to Cowling (1969), at least 12 mm. is necessary on dry soil to generate a significant response because old suberized roots are relatively ineffective absorbers of water and nutrients, and it takes 3 to 4 days for new roots to appear. Therefore, to start a growth cycle, rainfall must be sufficient to provide available storage beyond this recovery period; otherwise nutrient uptake is negligible. Soil micro-organisms, on the other hand, renew activity in a matter of hours after rewetting of dry soil (Funke and Harris 1968) and may thus add appreciable quantities of ammonium and nitrate ions to the inorganic pool even if the soil remains moist for no more than 2 or 3 days after rain (fig. 4, 40° C.). Without a concurrent plant response the added mineral N remains in the soil.

Taking into account what has been said about length of the soil-drying phase, its temperature, and the level of organic N present, such mineralization flushes would be expected to occur with greatest frequency and intensity in the immediate topsoil where number and amplitude of environmental fluctuations are maximum.

Nitrogen nutrition and saltbush production - an integration

Having elaborated on several major factors that influence nitrogen metabolism of the saltbush ecosystem, it remains to attempt a drawing together of the separate effects into a cohesive pattern of function that reflects climatic variability and efficiency of water use by the ecosystem. Nitrogen is stressed because it has proved to be the element most limiting in the nutrition of arid-zone communities generally. Other factors such as P and salinity could interact with and confound the relation between available N status and growth and, in certain circumstances, they undoubtedly do. But for the saltbush system under discussion there is no doubt that N exercises primary control over the fertility of the soil (Beadle and Tchan 1955) for chemical, microbiological, and plant measures of nitrogen status all correlate very closely.

Dry matter production per unit of evapotranspiration, a measure of the efficiency with which vegetation utilizes its moisture resources, is known to be strongly influenced by soil nutrient status, particularly at lower levels of fertility. Most significantly, an increase in yield produced by raising soil fertility does not produce a corresponding increase in evapotranspiration. In fact, large differences in yield brought about by fertilizer applications may result in only minor changes in evapotranspiration (Black 1966). Thus, just as fertilizer practices play a major role in nutrition and conservative use of water by cultivated crops, so environmental fluctuations that regulate mineralization of organic residues and the size of the inorganic nutrient pool would be expected to affect efficiency of dry matter production in most natural, terrestrial ecosystems, especially those of low nutrient status in dry areas. Unfortunately, information on this subject that relates specifically to shrub communities of arid lands is meager. Nonetheless, several observations and results of experimental work indicate that the general principles determined for farming systems also apply here.

Experimental confirmation of the importance of N in conservative use of water by *A. vesicaria* was obtained long ago by Trumble and Woodroffe (1954) when they measured a transpiration ratio of 570 for plants growing in soil of low-N status but only 370 in a soil of moderate-N content. These values convert to 3.5 and 5.4 cwt. of dry forage produced per acre-inch of water transpired. Related work by Trumble (1932) with *A. semibaccatum* showed that the transpiration ratio of this species also fell as N supply increased. Thus, a decrease in the ratio from 355 to 301 was observed when the soil was amended with sufficient NO_3-N to generate a production increase of 75 percent on the control.

Other observations indicate that the same nutritional control is important in production regulation in the field. For instance, to return to a comment made earlier, fertility status of arid-zone soils may appear to be high if assessment is based solely on those dramatic flushes of growth that occur sporadically after unusually favorable rains. But a different judgment will result if 2 good years follow in succession, for it is more than likely that production in the second year will be much less even though rainfall is similar in amount and distribution to the first (Trumble and Woodroffe 1954; Charley 1959). The simplest explanation for this evidence of variable water-use efficiency is fluctuation in inorganic nutrition of the vegetation and, in the saltbush communities, N nutrition in particular. Continued presence of available moisture in the soil allows growth to continue until a large fraction of labile N capital in the system is transferred to standing crop and subsequently plants are limited by a slow release of N from remaining, more resistant fractions of the organic pool. Until the soil is refreshed with readily decomposable N by litter return and incorporation, this situation of sluggish mineralization will remain to limit production. That, anyway, would seem to be true for abnormally wet periods. But what of the "normal" climatic

regime characterized by long periods of dryness interrupted by small, ineffective showers and an occasional large fall? Here a brief reiteration of important attributes of the saltbush system seems an appropriate means of providing perspective for analysis.

Some static and dynamic properties of the ecosystem

1. Rainfall is erratically distributed and composed chiefly of small showers. Winters are mild, but in summer temperatures and potential evaporation are high.

2. Plants do not respond significantly to rainfalls of less than about 12 mm., but soil micro-organisms renew activity rapidly when the soil is wetted even by light showers.

3. The environment is such that surface soil is dry most of the time, and saltbush depends for its survival on moisture stored in the subsoil by infrequent, heavy rains. Most root development is, however, in the surface horizons, particularly under the foliage.

4. Mean N status of the saltbush soils is low, but shrub growth and litter fall concentrate most labile mineral reserves in the first few centimeters of soil beneath the canopy. As a result, fertility here is much higher than either in subsoil or in the surface soil between shrubs. Nitrogen mineralization is greatest beneath shrubs, and community nutrition very much depends upon patterns and rates of transformation in these microsites.

5. Soil micro-organisms responsible for production of mineral N are more tolerant of moisture stress than plants. Their activity is enhanced by increasing the temperature and length of drying of the soil prior to wetting up.

6. Nitrogen content of saltbush litter is high and decomposition rate is rapid. Release of mineral N in the soil is also rapid if N status is high, but it declines with total N content.

7. In soils that have been dried for some time and then wetted, N mineralization is characterized by a short-lived burst of activity followed by a slower, steady rate of release to the inorganic pool. This pattern can be repeated a number of times, but with each cycle the initial flush becomes smaller as the labile organic pool is truncated.

8. Dry matter production per unit of water transpired is increased by improving N nutrition of the vegetation.

A simple functional model

Integrating these various static and dynamic system properties for a typical rainfall sequence of several ineffective showers followed by a large one, we can reasonably expect something like figure 7 to emerge, as the relation between water, nitrogen, and dry matter production.

Curves $Ap_{,N}$ and $Bp_{,N}$, for phytomass and inorganic N, respectively, respond to the inputs of the arrowed dots marked either ab, b, or a. These comprise two rainfall sequences, one consisting of a plant-ineffective fall followed by an effective fall, the other of four ineffective falls and an effective one. All rains are assumed to start microbial activity in the soil, but only the larger ones are supposed to be sufficient to promote and sustain a relatively lengthy period of active plant growth. Curves A_P and A_N reflect phytomass and inorganic N changes induced by rainfall sequence

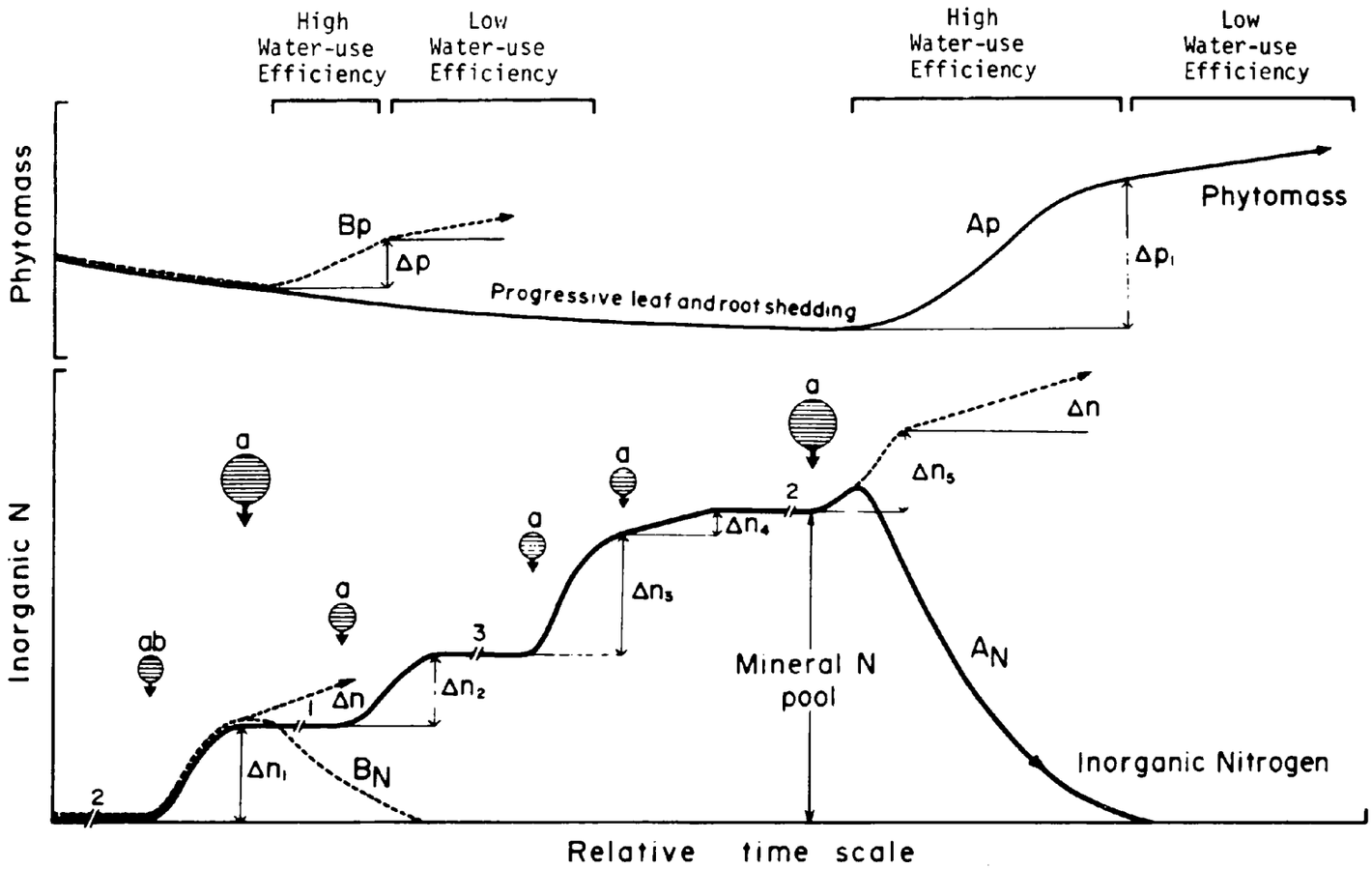

Figure 7.--Schematic relationship between rainfall distribution, inorganic nitrogen pool of the soil, and vegetation production efficiency with respect to water use.

(a); curves B_P and B_N depict responses to sequence (b); Δ_P and Δ_N represent phytomass and inorganic N increments, respectively. The number sequence 2, 1, 3, 2 along the curve A_N represents relative lengths of dry periods between rains where surface soil is dry.

At the commencement of the climatic sequence, growth water has just disappeared from the top of the profile and the saltbush is subsisting on subsoil reserves. Surface soil is very dry, and leaf and root shedding proceed to reduce standing crop from the peak generated by the last good rain.

After a dry period of 2 units of time, which may represent something like 2 or 3 weeks, a light rain falls. No vegetative response is observed, but microbial activity begins almost immediately and before the surface has dried out again a small pool of inorganic N has been generated. The mineralization rate is shown to include an initial burst followed by a decline that coincides with exhaustion of the labile fraction of organic N resulting from predrying--the decline also coincides approximately with exhaustion of available moisture in the surface soil. If at this time a plant-effective rain occurs, mineralization continues at a low rate because all labile organic N has been used and only more resistant fractions remain. After a lag of several days plant growth resumes, initially at a relatively high rate because of the available pool of inorganic N. However, as Δ_{n1} is small, plant drawdown soon removes this mineral supply and subsequent growth shifts to a condition of low water-use efficiency because of N shortage; if total N status of the soil is high, N deficiency may not occur because the basal rate of mineralization of resistant organic N may be fast enough to meet potential demands. Ordinarily, however, in these low-N soils, this basal rate is insufficient to maintain adequate nutrition and production of phytomass per unit of water transpired is poor.

Turning to rainfall sequence (a), we see what amounts to a fairly typical chain of events for the environment of the Western New South Wales saltbush country. Here an initial dry period of 2 units sets the stage for rapid mineralization. The following small shower then results in conversion of Δ_{n1} units of organic N to inorganic as before. Now, however, a further drying of 1 unit of time again preconditions the organic N pool for a flush of microbiological activity so that when the second light fall arrives mineralization is brisk and Δ_{n2} results. This second burst of activity should not be as great as the first because the precondition drying is less severe and because the residual store of organic N is already less than initially by an amount equal to Δ_{n1}. A third dry phase of 3 units and a small shower cause a larger mineral N increment (Δ_{n3}) than in the second because it would be expected that the additional severity of the prior desiccation could overcome the lowering of mineralization due to reduction of the organic pool by $\Delta_{n1} + \Delta_{n2}$. The small shower coming immediately after cessation of activity in the third wet-dry cycle sets off a minor transformation without an initial burst because there has been no preconditioning by drying and hence little if any labile organic N for the micro-organisms to work on. Further, the Δ_{n4} increment to the inorganic pool is small also because a relatively large amount of organic N has already been mineralized in previous activity phases; substrate for ammonification and nitrification is becoming limiting in the same way as was evident in the high-N curve of figure 5. Yet a subsequent drying for 2 units of time renders a proportion of residual organic N labile so that the terminating, plant-effective rain after this desiccation allows production of the significant Δ_{n5} increment from this available substrate; the fifth increment is shown as less than the first, which also follows a drying of 2 units, for the reason that organic N is by now depleted by a relatively large amount and only a longer drying would be sufficient to overcome this influence on mineralization. Inorganic N production rate after the Δ_{n5} flush should remain more or less constant for the remainder of the time for which growth water is available to the vegetation.

At the final, effective rain, when plant growth resumes it does so under conditions of high water-use efficiency by virtue of an existing pool of readily available mineral nitrogen. This situation will persist for as long as some part of the aggregate of the five mineralization increments remains; thereafter production will be at a lower rate dependent upon the rate of the linear phase transformation from "non-labile" organic N residues. In contrast to the events of the (b) rain sequence, the increase in phytomass resulting from the (a) pattern will be greater even though the amount of effective rain is the same simply because more of the total growth time is taken up with production unhindered by nutritional stress.

With repetition of rainfall sequences such as (a), the predrying stimulatory effect would be expected to gradually decline as the organic N pool is truncated. But, under normal circumstances, litter return of organic N should replenish the labile organic reserve with material susceptible to the desiccation effect. If so, the system as a whole, or more particularly the unit cells, should continue in a state that retains the potential for efficient production from larger rains, provided these are always preceded by minor "mineralization" showers.

Shrub response to fire

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General effects

The general effect of fire on shrubs should always be considered in relation to the ecological potential of a community. In grasslands, shrubs have a difficult time maintaining a dominant position due to competition from healthy grasses, droughts, and occasional fires. However, when domestic livestock graze these grassland areas, competition from grasses is lessened, fires are less frequent, and shrubs increase. Grazing reduces the competition from grass after burning, and the natural, or detrimental effect of fire on shrubs is lost.

Shrub seedlings compete directly with grasses for water and nutrients and many will die from direct competition (Martin 1966). Fire, alone, is sufficient to continually suppress the older plants and some of our recent work on honey mesquite *(Prosopis glandulosa)* indicates that the combined effect of fire, drought, and competition can be lethal.

In chaparral communities the climax vegetation is dominated by shrubs, and these communities retain their identity as plant associations and hold their ground despite burning (Hanes 1971). Without fire, the stands become stagnant and unproductive and give no evidence of being replaced by any other group of plants. Their vigor, however, is greatly enhanced by an occasional fire (Hanes 1971).

Following holocausts in forests, it is only natural for secondary succession to go from grasses and forbs for the first few years to shrubs for 5 to 50 years and finally to trees (Lyon 1969). Thus, we can understand how the boundaries of chaparral communities in California, barrens in northeastern United States and heathlands in Britain are extended by fires. Lacking recurrent fires, the shrubs become decadent and are replaced by trees. Obviously, succession is at work, and this is why our shrub-loving game animals such as deer, elk, and moose thrive in forest communities that have a recent fire history.

Regardless of where we find sprouting shrubs (grasslands, chaparral, or forest communities), as a group they are relatively fire tolerant. Excluding competition from grasses and droughts in the grasslands, very few sprouting species of shrubs are seriously harmed by fire for more than 10 years. Nonsprouting species that regenerate primarily through seeds are less tolerant of fires.

Most shrubs that depend on seed for reproduction produce numerous seedlings after a fire and are often enhanced by fire (Gratkowski 1961), provided that the fires are not frequent. However, if fires are too frequent, many species that are dependent on reproduction by seed may be destroyed completely. This is especially true for some chaparral species in California (Biswell 1969), and big sagebrush *(Artemisia tridentata)* in the Northern Desert (Pickford 1932).

Nonsprouting juniper (*Juniper* spp.) can also be destroyed by frequent fires, which would explain why juniper is not a climax species on grasslands but is climax on rocky breaks where it is protected from frequent fires (Burkhardt and Tisdale 1969). Since nonsprouting species require many years to set seed (Hanes 1971), a burning frequency of less than 15 years has been considered most desirable for the maintenance of these shrubs (Biswell 1969). Otherwise, a change in the relative frequencies of various species of shrubs following fire will occur as has been reported by Buell and Cantlon (1953) in New Jersey and Horton and Kraebel (1955) in California.

The woodland savannahs that did not evolve as a result of frequent fire will change to shrub communities if the frequency of fire is increased. In central Texas, mesquite savannahs change to shrub-grasslands after fire; in west Texas and eastern New Mexico, where fires have probably been more frequent, mesquite (the same species) has always existed as a shrub (Malin 1953). Likewise, mopane *(Colophospermum mopane)* in South Africa is changed from a tree to a shrub by frequent fires (Brynard 1965). Aspen *(Populus tremuloides)* and willow (*Salix* sp.) can also be maintained as shrubs by frequent burning. The foliage of these species is not very fire resistant and flares up easily.

Fire has caused some plants to develop certain physiological and morphological adaptations (Waibel 1948). For example, many small tree and brush types in Brazil's grasslands have very thick bark (the thickness equal to the diameter of the woody part in many cases) while the same plant in the adjoining forest has a thin bark. The babaca and the guararoba (*Coco* sp.), because of their fire resistant outer cover, are often the only large plants found on frequently burned grasslands (Waibel 1948).

Another adaptation to fire by shrubs may be caused by the increase in available nitrates and other minerals. Hesselman (1916) and Uggla (1958) reported that raspberry *(Rubus idaeus)*, common after fires, requires and accumulates very large quantities of nitrates in its tissues. Almost all berry plants are fire resistant and are rejuvenated by fire.

Forage yields of most sprouting shrubs are reduced for the first few years after a fire, but they regain their original stature in 2 to 25 years, generally in about 10 years. In the southeastern United States, gallberry *(Ilex glabra)* and saw-palmetto *(Serenoa repens)*, the two principal shrubs, recover in 2 or 3 years after burning (Hilman and Hughes 1965). In Arizona, the crown cover of burned chaparral was approaching that of the unburned area at the end of 7 years (Pond and Cable 1962). In the Pine Barrens of Wisconsin, Vogl (1970) suggested reburning every 10 years to maintain shrubs in a vigorous state for wildlife. Heathlands in Scotland should be burned every 10 to 15 years for maximum productivity (Gimingham 1970). After burning occurred in the boreal forest on the Kenai Peninsula, Alaska, desirable browse (principally *Salix* sp.) production for moose lasted for 5 to 20 years (Spencer and Hakala 1964). In south Australia, Cochrane (1963) found that the indigenous shrub stratum of sclerophyll forests reached the climax stage 7 to 10 years after a fire. Ives (1941) found that in the Colorado Headwaters area, brush reaches its maximum density 25 years after a burn.

Desert communities

Historically, fires have never exerted an important influence on the desert areas of North America (Humphrey 1962) except where grasses are abundant enough to carry fires (Griffiths 1910). Many of our deserts such as the Salt Desert and the Chihuahuan are essentially shrub-producing areas and support only a little grass. Grass is essential to carry fire any great distance except for the unusual case where shrubs are very close together. Although grasslands adjacent to deserts have burned at varying intervals, these fires stopped at low-precipitation areas where fuel was inadequate to carry the fire (Humphrey 1962).

Northern desert grass-shrub

Even when they are not prevalent, fires can have a devastating and long-lasting effect on shrubs in sagebrush-grass communities. Big sagebrush, a nonsprouter, is highly susceptible to fire (Pickford 1932; Blaisdell 1953). Blaisdell found that the production of this species on burned areas in Idaho was only 10 percent of that on the control 12 years after the burn. However, my observations at the U.S. Sheep Station in Idaho indicate that some areas recover more quickly. These differences may be related to the amount of seed produced by big sagebrush before a burn (Johnson and Payne 1968). Low sagebrush *(A. tripartita)* is also damaged by fire, but some plants resprout (Blaisdell 1953).

Antelope bitterbrush *(Purshia tridentata)* is severely damaged by burning (Blaisdell 1953; Pechanec and others 1954; Countryman and Cornelius 1957; Nord 1965). In Idaho 12 to 15 years after a burn, antelope bitterbrush was still only producing 50-60 percent as much as the control (Blaisdell 1953). If soil is wet at the time of burn or shortly after the burn, resprouting of this bitterbrush occurs regularly (Blaisdell 1953; Blaisdell and Mueggler 1956; Nord 1965). If the plants resprout, they will regain original growth in 9 to 10 years (Blaisdell 1953). Where fires are not followed by rain, antelope bitterbrush seldom sprouts. However, in southern California, desert bitterbrush *(P. glandulosa)* resprouts vigorously and abundantly (Nord 1965) even when postfire rains are lacking.

Other species severely damaged by fire include serviceberry *(Amelanchier alnifolia)*, granita gilia *(Gilia pungens)*, and broom snakeweed *(Gutierrezia sarothrae)* (Pechanec and others 1954). Mountain snowberry *(Symphoricarpos oreophilus)* appears to be somewhat harmed by burning but shows no change 15 years after burning (Pechanec and others 1954; Blaisdell 1953).

Rabbitbrush (*Chrysothamnus* sp.), a common genera in the sagebrush-grass zone, is enhanced by fire (Cottam and Stewart 1940; Blaisdell 1953; Countryman and Cornelius 1957; Chadwick and Dalke 1965). *Chrysothamnus puberulus*, *C. bloomeri*, *C. lanceolatus*, *C. viscidiflorus*, and *C. nauseous* all respond similarly. Generally, production is reduced for 1 to 3 years after burning, then it increases dramatically. On the U.S. Sheep Station near Dubois, Idaho, burning reduced production 59 percent the first year after burning (Blaisdell 1953). Three years after burning, production doubled and was tripled at the end of 12 years (Blaisdell 1953). Similarly, Chadwick and Dalke (1965) found that the cover of *C. viscidiflorus* was four to nine times greater on 8- to 18-year-old burns on sandy soils in northeast Idaho. Production of *C. bloomeri* doubled 5 years after a burn in northern California (Countryman and Cornelius 1957).

Production of horsebrush *(Tetradymia canescens)* was reduced about 50 percent the first year after burning, but doubled at the end of 3 years (Blaisdell 1953). At the end of 12 years it had increased fivefold. After 30 years many of these plants were dying out (Harniss and Murray 1971). Fire greatly enhances the dominance of this species

Oregon grape *(Mahonia repens)* is also favored by burning, especially by intense burns (Blaisdell 1953).

Southern desert grass-shrub

Griffiths (1910) and Wooten (1916) believed that fires almost entirely prevented the establishment of undesirable shrubs in the Southern Desert. Griffiths stated that because of the slow growth of shrubs, he believed they could be controlled by fires that occurred only once in 10 years. Wooten (1916) working in the same area (Santa Rita Experimental Range, Arizona) saw occasional fires that were hot enough to kill mesquite trees 10 to 12 feet high. In his opinion, fire had been the only restricting influence on the spread of trees and shrubs. Although grasses recovered quickly from such burning, shrubs were usually just reappearing by the time another fire occurred.

One of the most prevalent species in the Southwest is velvet mesquite *(Prosopis velutina)*. This species is moderately affected by fire, depending on the size of mesquite and amount of fine fuel available for burning (Cable 1961, 1965, 1967; White 1969). Following a June 28, 1963, wildfire, Cable (1965) reported a 21-percent kill for mesquite less than 2 inches in diameter and a 10-percent kill for trees larger than 2 inches. Using artificial fuels for controlled fires, Glendening and Paulsen (1955) obtained a 52 percent kill on young mesquites having basal stem diameters of 0.5 inch or less. Only 8 to 18 percent of the larger trees were killed by fire. Reynolds and Bohning (1956) killed 9 percent of the mesquite trees by using a prescribed burn on June 30, 1952. In a wildfire near Sasabe, Arizona, White (1969) reported a 20-percent kill of mesquite trees in moderate and severe burns.

Occasionally, fire may be more damaging to mesquite than is normally expected. Humphrey (1949) has reported mesquite kills of 50 percent on the Beach Ranch Study and 75 percent on the Sierrita Mountain Study. After 15 years, Humphrey revisited these same areas and still found mesquite drastically reduced. High kills such as these reported by Humphrey are rare. Part of this variation in mesquite kills, however, may be due to the amount of fuel available. On areas having 4,500 lb./acre of fuel, fire killed 25 percent of the mesquites, but on areas having 2,200 lb./acre of fuel, only 8 percent of the mesquites were killed (Cable 1965). Also, summer burns are more damaging to the mesquites than winter burns (Glendening and Paulsen 1955; Blydenstein 1957).

Other shrubs only moderately affected by fire are false-mesquite *(Calliandra eriophylla)* and velvet-pod mimos *(Mimosa dysocarpa)* . Very few of these plants (2-10 percent) died on severe burns and no plants died on light and moderate burns (White 1969). Reynolds and Bohning (1956) found that false-mesquite recovered quickly following burning and after 4 years had greater crown density than on unburned areas.

Yucca *(Yucca elata)* can be adversely affected by fire. Humphrey (1949) reported a 25-percent kill following a wildfire on Sierrita Mountain. In general, however, most yucca species are tolerant of fires and appear to hold their position in various plant communities despite fire.

Ocotillo *(Fouquieria splendens)* and Wheeler sotol *(Dasylirion wheeleri)* are severely affected by fire (White 1969). In a June 1963, wildfire many plants of ocotillo died--67 percent in severe burns, 40 percent in moderate burns, and 50 percent in light burns. All of the Wheeler sotol in moderate and light burns survived. However, only 3 percent of the plants survived in the severe burn.

Larchleaf goldenweed *(Haplopappus laricifolius)* is also easily killed by fire (White 1969). Severely damaged plants were completely killed and did not sprout by the end of the second growing season. Only 10 percent of the moderately damaged plants survived following fire. About 90 percent of the lightly damaged plants survived the first growing season, but the number of survivors declined to 80 percent the second growing season.

Paloverde *(Cercidium floridum)*, broom snakeweed, and burroweed *(Haplopappus tenuisectus)* are three more species that can be severely damaged by fire. Humphrey (1949) reported a 90 percent mortality of paloverde on the Sierrita Mountain study. Mortalities on broom snakeweed and burroweed following a July control burn were 95 percent or higher (Humphrey and Everson 1951). Cable (1967) and Reynolds and Bohning (1956) have reported similar data for burroweed. After 6 years, Cable found that burroweed was only 25 to 30 percent of preburn density, although it fluctuated upward during wet years and downward during dry years. After 13 years, burroweed exceeded preburn densities.

Thornber (1907) noted that fire was effective in killing catclaw *(Acacia greggii)*, creosote bush *(Larrea tridentata)*, mormon tea *(Ephedra trifurea)*, and graythorn *(Condalia lycioides)*. Except for creosote bush, I don't know of any research studies on these species which document the extent to which these species are affected by fire. Creosote bush can resprout after burning; however, intense fires, particularly during June and July, will cause high mortality (White and Ehrenreich 1968).

Algerita (*Berberis trifoliata*), fourwing saltbush (*Atriplex canescens*), winterfat (*Eurotia lanata*), and skunkbush sumac (*Rhus trilobata*) resprout vigorously after fire (Dwyer and Pieper 1967). Wright baccharis (*Baccharis wrightii*), a highly palatable shrub, also appears to be unaffected by fire (Humphrey 1949).

Reynolds and Bohning (1956) studied the effects of prescribed fire on several species of cactus in Arizona. They reported that June fires killed 67 percent of barrel cactus (*Ferocactus wislizeni*), 44 percent of jumping cholla (*Opuntia fulgida*), 45 percent of cane cholla (*Opuntia spinosior*), and 28 percent of pricklypear cactus (*Opuntia engelmannii*). On the Beach Ranch following a wildfire, Humphrey (1949) reported that fire killed 50 percent of the jumping chollas bisnagos (*Echinocactus wislizeni*) and 75 percent of both on another study area. In another study by Cable (1967), jumping cholla, cane cholla, and pricklypear were reduced 63, 45, and 32 percent, respectively.

Desert blackbush (*Coleogyne ramosissima*), a nonsprouter, is very susceptible to fire and is slow to reinvade after fires in southern Nevada and Utah (Jenson and others 1960; Beatley 1966). Burning generally improves forage productivity, but we are still a long way from an appreciation of the total effect of fire on blackbrush communities (Jenson and others 1960; Bradley 1965).

Grassland communities

Historically, fire is thought to have played a role in suppressing woody vegetation on native grasslands (Sauer 1950; Ito and Iizumi 1960). Other researchers deny that fire played a major role in suppressing woody vegetation (Malin 1953; Wedel 1957; Hastings and Turner 1966). They argue that climate has played the major role in controlling brush and there are good data to support this argument. Albertson and Weaver (1945) surveyed the mortality of trees in the plains during the drought of the 1930's. Their studies of native trees in ravines from Oklahoma to Nebraska showed mortality rates (by actual counts) ranging from 30 to 93 percent among the deciduous trees (elm, ash, hackberry) and from 35 to 80 percent or higher, among juniper. Thus, if fire has played any role in controlling brush, it has been a minor one (Wedel 1957). During the last 50 years, however, overgrazing has masked the effect of climate and accentuated brush invasion (Hastings and Turner 1966).

In opposition to the well-entrenched point of view that the distribution of treeless grasslands is governed principally by climate, the wide distribution of scarp woodlands throughout the climatically diverse grassland province poses some difficult questions as stated by Wells (1970): "Regardless of local or regional variations in climate and regardless of the species composition of both woodland and grassland in the Plains region, the following relation holds: the rougher and the more dissected the topography, the greater the former extent and the current spread of woody vegetation at the expense of grassland. Over and above the droughty climate, which undoubtedly has been a contributing factor, it is the vast flat or rolling smoothness and continuity of surface of the relatively undissected sedimentary mantle that appears to have played a powerful role in the development of the great expanses of treeless grassland on the Plains. This is where wind-driven grass fires, whether ignited by lightning or by man, must be accorded a big position in maintaining a treeless grassland. The wavelike motion of a wind-swept grassfire across a flat or rolling plain could continue indefinitely until it was quenched by rain or checked by an abrupt break in topography."

As I have mentioned before, the effects that fire, drought, and competition from grasses have on shrubs in grasslands are difficult to separate. Together, these three forces can be devastating on shrubs in grasslands; but I don't think any one of the three forces is adequate to control the growth of shrubs. There is, however, no doubt in my mind that our flat grasslands experienced extensive wildfires in the past. An oldtimer told me the case history of one such wildfire in the Panhandle of Texas (Short-Grass Prairie). It occurred in the early 1900's and started on the old Spade Ranch and covered a swath 20 miles wide and 60 miles long. Similar reports have been documented by Jackson (1965). Knowing that these fires occurred 100 years ago, that the ranges were in good condition, and that droughts occurred, I can see how fires were given credit for controlling shrubs. We know that wildfires are not as frequent today as in the past. However, even if they were as frequent, they would have less effect on shrubs due to the added effect of grazing by livestock.

The Great Plains

In the Great Plains, extensive information about the effect of fire on shrubs is lacking. In the northern Great Plains, Vogl (1967) found scrub oaks (*Quercus ellipoidalis*) very abundant in Wisconsin prairies that had been protected from fire for 25 to 80 years. Smooth sumac (*Rhus glabra*), leadplant (*Amorpha canescens*), and buckbrush (*Symphoricarpos orbiculatus*) are prominent sprouters in the central Great Plains (Anderson 1965; Anderson and others 1970).

In the southern Great Plains, we have observed smooth sumac on several burns. It is a very vigorous sprouter following hot fires and seems to require fire for survival. Shrubs are much more plentiful than in the northern and central plains. Honey mesquite is the most common shrub or tree in these southern areas, and very difficult to kill by fire. I have yet to see a large living green mesquite tree that was root-killed by a natural fire. However, after a fire, spraying with 2,4,5-T, or drought has affected a community and top-killed the trees, then the trees become more susceptible to fire. We have obtained mortalities ranging from 6 to 32 percent on mesquite trees that were sprayed and top-killed prior to our burns. Moreover, the larger the trees, the easier they are to kill by fire if they have been top-killed by spray or drought (Britton and Wright 1971). Young mesquite trees can also be killed by fire, depending on fire intensity, as shown in table 1.

Fisher (1947) also studied the effects of fire on young mesquite. He found that fire was effective in controlling mesquite seedlings less than 1 year old, killing 31 percent of the plants; but that none of the plants older than this were killed by burning. Our data, as shown in table 1, indicate that the intensity of the fire will affect mortality and that even plants older than seedlings can be killed by high-temperature fires. Nevertheless, as young mesquite trees get older, they are difficult to kill by fire alone, and they sprout vigorously following fire.

Table 1.--*Susceptibility of mesquite trees to fire*

Age	Temperature (°F.)				
	200°	500°	800°	1100°	Control
	Percent of kill				
6 mo. (seedlings)	43	91	100	100	14
18 mo.	60	100	100	100	0
10 yr. (basal dia. 1/2 in.)	0	0	4	8	0

Drought alone can have a devastating impact on trees and shrubs (Albertson and Weaver 1945), and we have seen many mesquite trees on our study areas that are believed to have been killed by the drought of the 1950's. More recently, our work on sprayed trees that have resprouted indicates that fire in combination with drought may be devastating to mesquite. Following a spring burn in 1969 on 1,200 permanently marked mesquite trees, we observed a 10.8-percent mortality. A year later, in 1970, after a very dry spring, mortality increased to 17.7 percent while no trees died in the unburned control.

Fire and climate together, along with good competition from grasses, appear to have a very complex role in controlling mesquite, a shrub well adapted to fire. Other shrubs also sprout following fire on the Great Plains. Fourwing saltbush is a vigorous sprouter and appears to have fully recovered 3 years after a burn. Lotebush (*Condalia obtusifolia*) also sprouts after a fire, but regains its original position in a community much more slowly than fourwing saltbush. Littleleaf sumac (*Rhus microphylla*) and algerita sprout following fires, but we have no research data on these species.

Chickasaw plum (*Prunus angustifolia*) and aromatic sumac (*Rhus aromatica*) sprout vigorously after burning in the southern Great Plains (Jackson 1965). In the northern panhandle of Texas, sandsage (*Artemisia filifolia*) is a nonsprouter that comes back vigorously as a seedling after fire (Jackson 1965).

On sandy soils in the southern Great Plains, shinnery oak (*Quercus havardi*) is common and is extremely fire hardy (McIlvain and Armstrong 1966). Although burning generally increases the availability and palatability of forage on shinnery oak rangelands for 3 to 4 years, the net effect is to increase the density of shinnery oak about 15 percent (McIlvain and Armstrong 1966). Our experiences with shinnery oak in Texas also indicate that it is a strong sprouter and probably thickens following fire, although fire does maintain it as a low-growing shrub.

Cactus species in Texas are not as well adapted to fire as most of our woody plants. Tasajillo (*Opuntia leptocaulis*) is easily killed by fire (85- to 90-percent mortality). Pricklypear and cholla (*Opuntia imbricata*) are moderately harmed by fire. Heirman (1971) found that following chaining, fire killed 40 percent of the pricklypear plants the first growing season after burning. In an unchained area, fire killed 22 percent of the pricklypear plants. One of the major effects of fire on pricklypear was the reduction in pad numbers. Burning reduced the number of pricklypear pads by 66 percent (including current season's growth after the fire); however, pricklypear pads increased 83 percent in the control. Total cholla killed by burning was 19 percent (Heirman 1971). Cholla plants less than 1 foot in height experienced a greater kill (27 percent) than did those over 1 foot in height (12 percent).

Rio Grande Plains

In south Texas, shrubs are numerous, and most are vigorous sprouters. Fire is effective in reducing shrub cover for several growing seasons, although mortality, if any, is low (Box and others 1967; Box 1967; White 1969). White (1969) found that as fuel quantities increased, damage to individual species increased. Where fuel was less than 2,000 lb./acre, approximately 50 percent of the brush species were top-killed. Fuel levels of 2,000 to 4,000 lb./acre resulted in a top-kill of about 80 percent. At fuel levels over 4,000 lb./acre, top-kill was 100 percent. The size of brush species and the amount of damage caused by fire were inversely related.

Huisache (*Acacia farnesiana*) and blackbrush acacia (*Acacia rigidula*) are the most vigorous sprouters following fire (Box and others 1967). Mortality on these species and most others in south Texas varies from 0 to 14 percent. Burning during a dry year will cause mortalities ranging from 10 to 14 percent; whereas, burning during a wet year will cause very little mortality (White 1969).

Other common sprouters in south Texas are algerita, lotebush, brasil, honey mesquite, creeping mesquite (*P. reptans* var. *cinerascens*), mexican persimmon (*Diospyros texana*), granjeno (*Celtis spinosa*), prickly ash (*Zanthoxylum fagara*), and lycium (*Lycium berlandeii*).

Box and others (1967) reported mortalities of 33 and 40 percent for algerita and lotebush, respectively. However, these data were not supported by White (1969) who measured no mortality for either species. The major difference was moisture at the time of the burn; Box and others burned in the fall when the soil was dry and White burned during the early spring when the soil was wet. Possibly, some of the difference was due to season, although White (1969) attributed the different responses to soil moisture.

The relative abundance of shrubs changed following burning (Box and White 1969). Huisache, blackbrush, twisted acacia (*Acacia tortuosa*), and lotebush all increased in relative abundance; agarito, lycium, tasajillo, mesquite, and creeping mesquite all declined in relative abundance following burning.

Chaparral communities

Throughout the world chaparral is regarded by plant geographers as a fire-induced type (Shantz 1947). It is typical of Mediterranean climates and is known in the Mediterranean region and South Africa as macchia or fymbos, in southwest France as heath, in south Australia as brigalow-scrub, in Spain as tomillares, and in the Balkans as phrygana. Chaparral communities also exist in North Africa, Asia Minor, Mexico, and Central Chile. All of these communities are synonymous with our California chaparral, and the species depend and behave similarly to fire (Shantz 1947).

"That this type was ever free of fire seems unlikely" (Shantz 1947). Shantz further states that every plant species in chaparral communities survives because it is capable of passing through fire without being killed. The numerous brush seedlings after fire in chaparral stands (Sampson 1944; Sweeny 1957) as well as the vigorous sprouting ability of many species are unmistakable signs of their adaptability to fire (Phillips 1965; Hanes 1971).

Chaparral communities are generally bounded by forests on the upper boundaries and grasslands below. Though fire is part of the chaparral environment, and probably not necessary for its maintenance (Hanes 1971), fire carries this type far beyond its natural boundaries into forest communities. Thus, in forest communities, chaparral is induced by fire, but in true chaparral communities it is most likely induced by climate.

Without fire, chaparral communities become very unproductive. An old stand of decadent mixed-chaparral brush will produce 13 to 106 lb. of browse per acre yearly (Gibbens and Schultz 1963). After fall and early spring burns, these same communities will produce from 750 to 2,750 lb. per acre yearly (Biswell 1969).

California chaparral

By far the most abundant species in the California chaparral communities, particularly on south slopes, is chamise (*Adenostoma fasciculatum*). It is a vigorous sprouter and also germinates from dormant seeds. Shoots of chamise grow rapidly the first 5 years after top removal by fire (Sampson 1944; Horton and Kraebel 1955). By the sixth year, growth is slower and by the eighth year annual growth declines appreciably (Sampson 1944). Chamise growth slows down until it almost stops at 20 years (Horton and Kraebel 1955). In the absence of fire, old chamise chaparral is a "declining" climax that shows no sign of being replaced by another plant community (Hanes 1971). Communities must be reburned to remain vigorous and healthy.

Yerba santa (*Eriodictyon californicum*) is also common after fire and comes both from seed and an extensive rhizomatous root system (Sampson 1944; Hanes 1971). Other vigorous sprouting species common after fire, depending on the site, are California scrub oak (*Quercus dumosa*), deerbrush (*Ceanothus integerrimus*), toyon (*Heteromeles arbutifolia*), greenleaf manzanita (*Arctostaphylos patula*), Eastwood manzanita (*Arctostaphylos glandulosa*), silktassel (*Garrya veatchii*), and western mountain-mahogany (*Cercocarpus betuloides*). Species of lesser abundance that sprout vigorously after fire are laurel sumac (*Rhus laurina*), sugar sumac (*Rhus ovata*), chilacote (*Marah macrocarpus*), white-thorn chaparral (*Ceanothus leucodermis*), holly-leaved cherry (*Prunus ilicifolia*), redberry (*Rhamnus crocea* var. *ilicifolia*), poison oak (*Rhus diversiloba*), blueblossom (*Ceanothus thyrsiflorus*), and California huckleberry (*Vaccinium ovatum*).

The seedlings of many chaparral species are abundant after a fire. Seed from deerweed (*Lotus scoparius*), a low-growing dominant seral species, must be scarified by fire to germinate (Went, Juhren, and Juhren 1952). This species is particularly abundant in sunny locations on burns near the coast during the first decade and then diminishes, but only isolated individuals remain by the end of the second decade (Hanes 1971).

Other nonsprouting or weak-sprouting species that thrive on new burns as seedlings, depending on aspect, elevation, and proximity to the coast, are wedgeleaf ceanothus (*Ceanothus cuneatus*), hoaryleaf ceanothus (*C. crassifolius*), desert ceanothus (*C. greggii* var. *vestitus*), black sage (*Salvia mellifera*), white sage (*S. apiana*), California buckwheat (*Eriogonum fasciculatum*), California sagebrush (*Artemisia californica*), Stanford manzanita (*Arctostaphylos stanfordiana*), parry manzanita (*A. parryi*), common manzanita (*A. manzanita*), hoary manzanita (*A. canescens*), bigberry manzanita (*A. glauca*), mariposa manzanita (*A. mariposa*), wavyleaf ceanothus (*C. foliosus*), Lemmons ceanothus (*C. lemmoni*), goldenbush (*Haplopappus squarrosus*), and monkey flower (*Mimulus longiflorus*).

In the San Francisco Bay area, chaparral-broom (*Baccharis pilularis*) has become increasingly abundant due to exclusion of fire (McBride and Heady 1968). In a simulated burning study, eight out of 11 plants burned at the base died; small shrubs were killed more easily than large shrubs. These data were similar to those commonly observed on wildfires and give ample evidence that chaparral-broom is reduced, but not eliminated, by wildfires (McBride and Heady 1968).

Arizona chaparral

Some chaparral communities extend from California into Arizona. Following a wildfire near Globe, Arizona, in 1951, Pond and Cable (1962) found that shrub live oak (*Quercus turbinella*), sugar sumac, redberry, Wright silktassel (*Garrya wrightii*), and skunkbush sumac responded vigorously after fire. The cover was dominated by shrub live oak. Weak sprouters such as desert ceanothus and nonsprouters such as pointleaf manzanita (*Arctostaphylos pungens*) and pringle manzanita (*A. pringlei*) remained greatly reduced by fire 6 years after burning (Pase and Pond 1964).

Forest communities

Oak-brush

Gambel oak (*Quercus gambelii*) is a very fire-tolerant species. The most common effect of fire in west-central Colorado is to stimulate suckering with resultant thickening of open stands and merging of scattered stands into continuous thickets (Brown 1958). In Utah, McKell (1950) found that Gambel oak grew rapidly the first two growing seasons (50-percent recovery) after burning, but it had only recovered

75 percent of its original cover 18 years after a burn. The number of shoots, however, increased fourfold the first year after burning, and then declined until they were equal on both burned and unburned areas after 18 years. Oak tends to thin out and retreat when protected from fire (Brown 1958).

In addition to Gambel oak, McKell (1950) followed the rate of recovery of several other shrub species associated with Gambel oak on 1-, 2-, 9-, and 18-year old burns. Cover of chokecherry (*Prunus melanocarpa*) and Wood's rose (*Rosa woodsii*) exceeded that of adjacent unburned areas the second year after burning. After 18 years the cover of both of these species was twice as high on the burned area as the unburned control.

McKell found that snowberry (*Symphoricarpos vaccinoides*) was only slightly harmed by fire for the first few years after burning. However, after 9 years, both cover and plant numbers were nearly equal to those of the unburned area. The ninebark (*Physocarpus malvaceus*) recovery from fire was similar to that of snowberry.

Serviceberry recovers rapidly from fire but then gradually declines to 60 percent of the cover found on unburned ranges (McKell 1950). Part of this decline may possibly be due to an interaction between the effect of fire and use by big game. Oregon grape and mountain lover (*Pachystima myrsinites*) remained drastically reduced on burns after 9 years. But after 18 years, Oregon grape had increased threefold over unburned plots; mountain lover was still only 50-percent recovered.

Juniper

Juniper is a widely distributed shrub or small tree which occurs throughout the Western United States. All of the following nonsprouting species are highly susceptible to fire: one-seeded juniper (*Juniperus monosperma*); Utah juniper (*J. osteosperma*); Ashe juniper (*J. ashei*); rocky mountain juniper (*J. scopulorum*); western juniper (*J. occidentalis*); and eastern redcedar (*J. virginiana*). They are especially difficult to maintain in grasslands if fires occur frequently (Johnson 1962). That these species are invading grasslands because of overgrazing and the resultant lack of fires and competition from grass is well documented (Bray 1904; Foster 1917; Miller 1921; Leopold 1924; Emerson 1932; Cottam and Stewart 1940; Parker 1945; Allred 1949; Humphrey 1950; Jameson 1962; Johnson 1962; Arnold and others 1964; Burkhardt and Tisdale 1969; Blackburn and Tueller 1970). Since they are not fire-tolerant plants, nonsprouting juniper and shrub species generally occupy escarpments and other topographic breaks surrounded by grasslands (Emerson 1932; Wells 1970).

Juniper trees less than 4 feet tall are easily killed by fire (Jameson 1962; Dwyer and Pieper 1967); however, I have seen several wildfires where trees in excess of 12 feet were killed by crown fires. If a stand of old trees is burned, numerous seedlings often follow. Our experience with Ashe juniper shows that a second fire in these communities within 10 years after the first one will keep a grassland relatively free of juniper trees and shrubs for at least 20 to 30 years.

Redberry juniper (*J. pinchoti*) and alligator juniper (*J. deppeana*) are sprouting species and are very difficult to kill by fire. However, fires reduce the sphere of influence of these trees. Once a tree is established, it dominates the area around it and very little forage grows under the tree. When the trees are burned, they dominate less area, and grasses and forbs encroach.

Fire is a major factor in controlling the distribution of juniper. However, drought and competition from grass also affect establishment (Johnson 1962). Sometimes these factors are so closely related that we don't know which is the most important in the distribution of juniper. I agree with Johnson's (1962) statement that grass competition and fire play a dual role in limiting the distribution of juniper.

Ponderosa pine

Natural fires occur in ponderosa pine (*Pinus ponderosa*) every 5 to 10 years (Kallander 1969). Shrubs are killed back but many resprout vigorously and appear fully recovered 11 years after the fire (Weaver 1967). Shrubs sprouting vigorously after fire in the ponderosa pine zone on the west coast include ninebark, oceanspray (*Holodiscus discolor*), bittercherry (*Prunus emarginata*), willow, syringa (*Philadelphus lewisii*), serviceberry, snowberry (*Symphoricarpos rivularis*), rose (*Rosa spaldingii* and *R. ultramontana*), and spiraea (*Spiraea betulifolia*). Although these shrubs sprout vigorously under the pines, it appears to take 2 or 3 years for them to reach a stature that impels stockmen to again burn to reduce the rough growth (Weaver 1967). Bitterbrush is severely reduced by fire; bitterbrush was still not fully recovered 27 years after a wildfire on the Warm Springs Reservation in Oregon (Weaver 1967).

Douglas-fir

Shrubs are favored by fires in the Douglas-fir zone of the Intermountain region, and they have a dominant influence on plant communities for 20 to 50 years (Mueggler 1965; Lyon 1969). Species greatly enhanced by fire include scouler willow (*Salix scouleriana*), mountain lover (*Pachistima myrsinites*), serviceberry, rocky mountain maple (*Acer glabrum*), huckleberry (*Vaccinium* sp.), thimble-berry (*Rubus parviflorus*), and oceanspray. Scouler willow is especially abundant after burning (Mueggler 1965; Leege 1969). All of these species are sprouters and increase in density because root crowns of single plants produce multiple sprouts (Lyon 1966).

Other species favored by fire are elderberry (*Sambucus racemosa*), currant (*Ribes viscosissimum*), alder (*Alnus sinuata*), bittercherry, spiraea, redstem ceanothus (*Ceanothus sanguineus*), shiny-leaf ceanothus (*C. velutinus*), rose (*R. gymnocarpa*), cascara (*Rhamnus purshiana*), and syringa (Mueggler 1965; Lyon 1966; Leege 1969; Leege and Hickey 1971).

Shiny-leaf ceanothus does not resprout after fire, but it produces numerous seedlings (Lyon 1966). Fire breaks the seed-coat dormancy of this species (Sweeny 1967). Five years after a fire, shiny-leaf ceanothus was the most common species of brush on the Sagehen Creek Field Station, Nevada County, California (Bock and Bock 1969). Redstem ceanothus and bittercherry also produce many seedlings after a fire; in addition, the older plants resprout (Leege 1968).

Mountain ash (*Sorbus scopulina*) is eliminated by burning and will not reappear until birds bring new seeds (Lyon 1966). Snowberry (*Symphoricarpos oreophilus*) and swamp gooseberry (*Ribes lacustre*) do not appear to receive any long-term benefit or harm from fires.

In the Douglas-fir zone on the west coast of the United States, the shrub genera are similar to those of the Rocky Mountains and respond similarly to fire. *Arctostaphylos* sp. is the only genera not reported in the northern Rocky Mountains and one species on the west coast, red bearberry (*Arctostaphylos uva-ursi*), increases in frequency after fire (Neiland 1958).

Southern mixed forest

Shrubs that respond vigorously to fire in the Southeast include saw-palmetto, seminoletea pawpaw (*Asimina reticulata*), yaupon (*Ilex vomitoria*), common sweetleaf (*Symplocos tinctoria*), American beautyberry (*Callicarpa americana*), and American cyrilla (*Cyrilla racemiflora*). At the end of the second growing season, all of these shrubs usually produce more on the burned than on the unburned areas (Hilman and Lewis 1962; Lay 1967). Winged sumac (*Rhus copallina*) and blackberry (*Rubus* sp.) also appear to be stimulated by burning (Duvall 1962). Fires produce a definite and long-lasting increase

on Virginia creeper (*Parthenocissus quinquefolia*) and poison ivy (*Rhus toxicodendron* var. *vulgaris*) (Oosting 1944).

Several kinds of shrubs are harmed by repeated burning. Lotti (1956) found that 90 percent of southern waxmyrtle (*Myrica cerifera*) is killed with four annual fires. Similar results have been reported by Givens (1962). Gallberry is also severely harmed by fire based on results 1 year after burning (Burton and Hughes 1961; Hilman and Lewis 1962) and 7 years after burning (Halls and others).

Other species which show decreased production 2 years after a fire include American holly (*Ilex opaca*), farkleberry (*Vaccinium arboreum*), flowering dogwood (*Cornus florida*), Kentucky viburnum (*Viburnum molle*) (Lay 1967), gopherapple (*Chrysobalanus oblongifolius*) (Hilman and Lewis 1962), and *Baccharis* (Givens 1962).

Oak - hickory - pine forest

In pine forests of Piedmont, North Carolina, Oosting (1942) found that the only shrub seriously affected by fire was downy viburnum (*Viburnum affine* var. *hypomalacum*) which was reduced more than 80 percent. All other shrubs and vines remained essentially the same as before except that rose (*Rosa virginiana*) was added to the lists after fire. Also, blackberries soon become abundant after fire. Among hardwood trees, winged sumac and sometimes sassafras (*Sassafras officinale*) are apt to be locally abundant after fire (Oosting 1942).

On cut-over spruce stands in the higher southern Appalachian Mountains, the vegetation within a year after fire is frequently a dense, rank growth of blackberry and raspberry briers. This is promptly followed by an abundance of pin cherry (*Prunus pensylvanica*), a shrub, and resprouts of yellow birch (*Betula lutea*), a tree (Korstian 1937). The cherry, because of its rapid early growth, usually gains a dominant position in the new stand and holds it for 15 to 20 years. Tall shrubs such as rhododendron (*Rhododendron catawbiense* and *R. maximum*), mountain laurel (*Kalmia latifolia*), serviceberry (*Amelanchier canadensis*), and huckleberry (*Vaccinium* sp.) contribute to the great density of the young stand, although as a rule they occupy subordinate positions.

In South Carolina, scrub oak (*Quercus* sp.) is a vigorous sprouter in the sand hills (DeCoste and others 1968).

Northeastern broadleaf forests

In the northeastern United States forests, blueberries (*Vaccinium angustifolium, V. myrtilloides,* and *V. vacillans*) persist for years in the understory of unburned communities as decadent plants. For maximum production of forage and particularly berries, they must be rejuvenated periodically by removal of dead or decadent stems and clones (Sharp 1970). Brown (1960) found blueberries consistently more prevalent on areas with a fire history than on adjacent unburned communities.

Moderate burns (an intensity of 362° C. and 40 sec./sq. meter duration) are the most desirable for increasing the density and productivity of these plants (Smith 1968). Severe burns are harmful (Ahlgren 1960; Smith 1968).

Following the first burn, it requires three growing seasons to bring these clones of blueberries to a satisfactory level of nutrition and vigor (Buell and Cantlon 1953; Sharp 1970), although vegetative shoots may be abundant 1 year after a fire (Skutch 1929). Other researchers seem to agree. Ahlgren (1960) mentions that after a fire, blueberries reach a position of dominance more slowly than other species. Vogl (1964) states that infrequent fires are more desirable for production of blueberries than frequent and repeated fires.

For commercial blueberry production, Trevett (1962) recommends rotation burning, then no burning during two berry crop years followed by burning once again. This rotation means burning every fourth year. However, blueberries in wildlands cannot be managed by this plan because grouse need to feed on the buds during the winter (Sharp 1970).

Most berry plants follow fire and are favored by burning. Blackberry (*Rubus* sp.) and raspberry (*R. idaeus*, *R. pubescens*) plants are very resistant to burning and are consistently more abundant on burned areas (Ahlgren 1960; Vogl 1967; Doerr and others 1970; Swan 1970). Seedlings of these species appear in high densities after a fire (Sharp 1970). Gooseberries (*Ribes glandulosum*) are found only on burned areas and begin to decline about the third or fourth year after burning (Ahlgren 1960). Raspberries also begin declining the third or fourth year after burning. Cranberries (*Viburnum edule*) are well on their way to recovery 1 year after burning (Doerr and others 1970).

Conflicting reports have been presented on the effect of fire on huckleberries (*Gaylussacia baccata*). Buell and Cantlon (1953) found that the cover of huckleberry was approximately 40 percent in unburned communities and only about 3 percent in plots burned annually. Full recovery did not occur until 10 to 15 years after burning. On 25- to 30-year-old burns, Brown (1960) found huckleberries consistently more prevalent than on unburned areas. Strang (1970) on the other hand reported that within 2 years after a fire on rocky heathlands in western Nova Scotia, huckleberries and other shrubs had recovered to the point where the burned area was scarcely distinguishable from its surroundings. Swan (1970) found huckleberries to be neutral to fire within 26 months after burning.

Hazel is a common upland shrub in the northern pine-hardwoods that responds vigorously to fire (Vogl 1967, 1970; Swan 1970). Beaked hazel (*Corylus cornuta*) tends to occupy mesic sites while American hazel (*C. americana*) occupies drier or more xeric sites; however, many exceptions to this can be found (Buckman 1964). Both species reproduce by seedlings, sprouts, underground stems, and layers (Hsuing 1951), but the most important means of complete colonization is vegetative reproduction from underground stems (Buckman 1964).

Aerial stems of hazel are easily killed by fire, regardless of how gentle the flames or frequent the burning (Buckman 1964). However, prolific sprouting follows spring burning, and the original stand of brush is replaced in stature and number of stems in only a few years. On all spring burning treatments (1-, 2-, and 4-year treatments), Buckman recorded at least twice as many sprouts per acre as in the control. On summer burns, however, he noted a reduction in vigor of sprouts. After four consecutive summer fires, the number of sprouts declined to one-tenth the number occurring in the companion spring-burned treatments.

Buckman (1964) believed that repeated summer fires could lead to the eventual destruction of all hazel clones. Similarly, when the humus is sufficiently dry to be consumed, single hot summer fires may eliminate hazel since nearly all of the underground rootstocks are in the morhumus, lying at or very close to the contact zone with mineral soil (Buckman 1964). Ahlgren (1960) observed a delayed response of beaked hazel sprouts after a severe fire. He attributed the delayed response to heat damage on the underground parts.

As burning becomes more frequent in the New Jersey pine region, shrub oaks (*Quercus elicifolia* and *Q. prinoides*) become more plentiful in the shrub layer (Buell and Cantlon 1953). In Rhode Island, Brown (1960) found that *Q. elicifolia* was the most numerous species among the secondary trees and shrubs on 25- to 30-year-old burns.

Several authors agree that other shrubby species in the Northeast that recover quickly after fire include alder (*Alnus crispa* and *A. rugosa*), willow, pin cherry (*Prunus pensylvanica*), Juneberry or shadbush (*Amelanchier* sp.), steeplebush (*Spiraea*

tomentosa), and chokecherry (*Prunus virginiana*). Leatherleaf (*Chamaedaphne calyculata*) is abundant during the quaking-bog stage after fires in white cedar-hardwood swamps (Little 1964). Sand cherry (*P. pumila*), corralberry (*Symphoricarpos orbiculatus*), redroot (*Ceanothus ovatus*), and sweet fern (*Myrica asplenifolia*) are also common sprouters after a fire but may decrease with frequent and repeated fire (Vogl 1970). Juneberry can also be harmed by frequent and repeated fire (Vogl 1970).

Strang (1970) implies that broom crowberry (*Corema conradii*) and Rhodora (*Rhododendron canadense*) are fire tolerant in western Nova Scotia. Although not very prevalent, winged sumac and hawthorn (*Crataegus* sp.) appear to be favored by burning (Brown 1960). Sharp (1970) noted that seedlings of sumac, wild grape (*Vitis*), and elderberry (*Sambucus*) occurred in a random pattern throughout spring burns, but not on unburned areas. New Jersey tea (*Ceanothus americanus*) is also more common in burned than unburned communities (Swan 1970).

Rose (*Rosa acicularis*) is less fire tolerant than many species of shrubs and was relatively infrequent on all burns except those which were lightly burned (Ahlgren 1960). By contrast, Doerr and others (1970) reported *Rosa* spp. to be well on its way to recovery 1 year after a fire; this is typical of the effect of fire on rose in most plant communities.

Labrador-tea (*Ledum groenlandicum*) appears to be somewhat harmed by fire (Ahlgren 1960). Likewise, honeysuckle (*Diervilla lonicera*) (Swan 1970) and teaberry (*Gaultherica procumbens*) (Buell and Cantlon 1953) decrease after burning. The short- and long-term effect of fire is harmful to witch hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*), bluebeech (*Carpinus caroliniana*), flowering dogwood (*Cornus florida*), wild-raisin (*Viburnum cassinoides*), maple-leaved viburnum (*V. acerifolium*), sweet pepperbush (*Clethra alnifolia*), black highbush blueberries (*Vaccinium atrococcum*), and mountain-holly (*Nemopanthus mucronata*) (Brown 1960).

Conclusions

In general, fires suppress shrubs in grasslands, promote them in forests, and stimulate them in chaparral communities. However, we should always evaluate the effect of fire on shrubs in relation to age of plants, soil moisture at time of burn, intensity of the fire, season of burn, health of herbaceous plants (particularly grasses in grasslands), and the frequency of droughts. All of these factors can, and usually do, affect the response of plants to fire. If we wish to maintain healthy plant communities, plant dormancy and good soil moisture before burning are essential to minimize damage to plants.

In the management of shrubs, total production is of less interest to us than a maximum sustained forage that is usable by game animals. For this reason, the burning of many shrubs is necessary for the most productive ecosystem that will be of maximum benefit to mankind.

Insects and diseases of shrubs on western big game ranges

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Big game in Western United States rely heavily on shrubs for food and shelter. The kinds, amounts, and condition of shrubs greatly affect condition and survival of game during the winter when migratory species concentrate at lower elevations, where they occupy a relatively small area, perhaps one-tenth as great as they occupy during the summer.

In this report, we illustrate the impact of harmful insects and diseases on shrubs by citing information of the following species, which are among the more preferred shrubs found on winter ranges in the West--serviceberry (*Amelanchier* spp.), ceanothus (*Ceanothus* spp.), mountain mahogany (*Cercocarpus* spp.), bitterbrush (*Purshia tridentata*), and willow (*Salix* spp.).

Our information is derived from a combination of original observations and a review of the literature. Species of insects occurring on browse shrubs in Idaho and adjacent States have been collected and identified by us beginning 7 years ago (fig. 1). A few species have been studied in some detail. During this same period, we have studied rust diseases of shrubs, and recently have begun to study other diseases.

Figure 1.--Insects associated with browse plants were either reared, hand picked, or obtained by beating into a net. The damage potential of many insects has not yet been assessed.

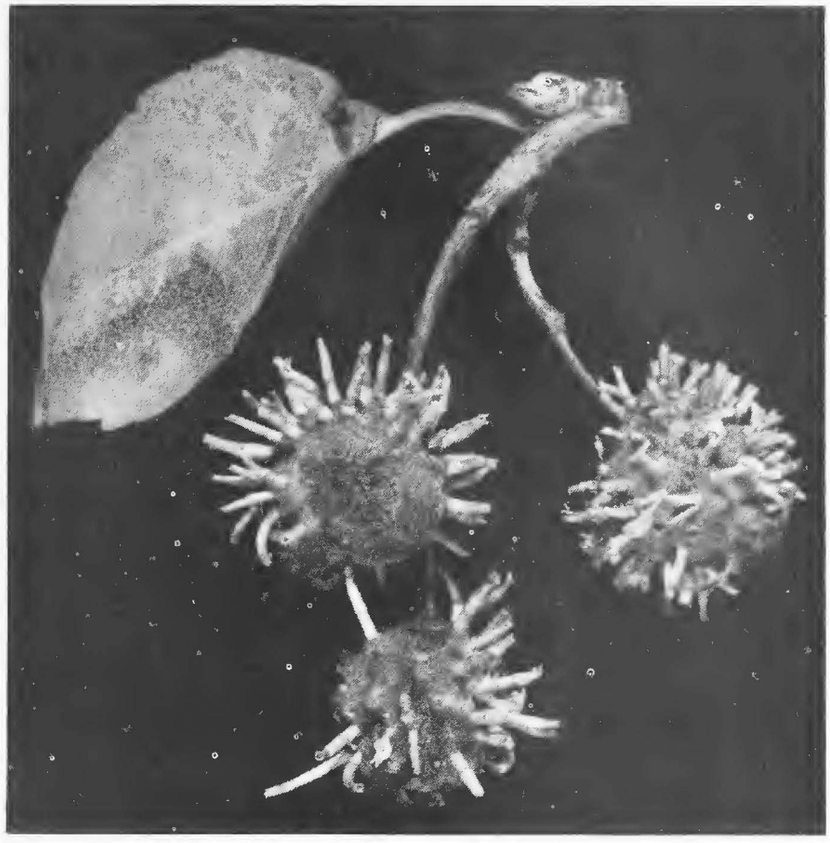

Figure 2.--Aecia of Gymnosporangium inconspicuum *Kern on fruit of Utah serviceberry. This is probably the most common disease of serviceberry in the Great Basin.*

We recognize that research on pests of wildland shrubs is in its infancy; but our experience already makes it apparent that much new information is needed if we are to derive optimum benefits from wildland shrubs.

Amelanchier

The young foliage of serviceberry (*Amelanchier* spp.) is particularly choice browse for deer, elk, and livestock, but even after autumn leaf fall its stems are a source of feed. Serviceberry also produces fairly abundant crops of fruit that are consumed by mammals and birds.

We have identified 12 species of insects and at least 20 species of fungi that infest *Amelanchier* spp. in the West. Also, serviceberry is quite sensitive to air pollution and evidence from the East (Hilborn and others 1965) suggests that it might harbor viruses.

Serviceberry seems to have escaped large scale destructive infestation by insects, but defoliators and stem insects cause severe damage locally. A common insect is the western tent caterpillar, *Malacosoma californicum* (Packard), and its subspecies *M. c. lutescens* (Newmoegen and Dyar) and *M. c. pluviale* (Dyar) (Stehr and Cook 1968). Tent caterpillars can severely defoliate individual plants but infestations seldom persist long enough to cause lasting damage. Also affecting leaves is a midge, *Trishormomyia canadensis* Felt. It causes unusual conical galls that protrude from the undersurface but they do not cause observable harm. The oyster shell scale, *Lepidosaphes ulmi* (Linn.), can weaken or kill branches by sucking sap from them. The scale could have been introduced into North America many years ago and has caused extensive harm to several shrub species in western States. Fruits of serviceberry also are often infested by a sawfly (*Hoplocampa* sp.).

Gymnosporangium rusts cause early defoliation, shoot dieback, and malformation of serviceberry fruits (fig. 2). Therefore, rusts are presumed to decrease both quality

and quantity of browse for big game and possibly impair natural regeneration by reducing crops of viable seed. In some years, rusts become epidemic over large areas. McVaugh (1942) noted that because of rusts: "In some areas...of the Great Basin the *Amelanchier* fruits may be so heavily infested that it is almost impossible to find one maturing normally...." Epidemics develop when favorable moist weather coincides in spring and early summer with abundant inoculum on Cuppressaceae alternate hosts such as junipers and incense cedar (Peterson 1967).

Inasmuch as the rusts lack a repeating spore stage on serviceberry, they cannot intensify without alternation. Unfortunately though, junipers are common associates of serviceberry on many western game ranges and weather often favors at least scattered infections. In planning rehabilitation projects that include serviceberry, it is well to bear in mind that rusts can spread 1 to 2 or more miles from juniper to serviceberry (MacLachlan 1935).

Ceanothus

The genus *Ceanothus* includes many important browse species in Western United States: *Ceanothus velutinus* Dougl. and *C. martini* M. E. Jones in the Great Basin area; *C. sanguineus* Pursh in the northern Rocky Mountains; and *C. integerrimus* H. & A. and others in the Pacific Northwest. Although ceanothus is still abundant throughout the West, concern exists that such stands are declining because of successional changes and decadence resulting from fire protection practices and attacks by insects and diseases.

The most prominent defoliator of ceanothus is the California tortoise shell butterfly, *Nymphalis californica* (Boisd.). Destructive outbreaks have occurred in many northern California localities, especially during 1911, 1932, and 1951. During 1959, caterpillars severely defoliated *C. velutinus* in the Cascade Mountains of Oregon; during the same year and again in 1961, similar damage occurred in southwestern Idaho. The western tussock moth, *Orgyia vetusta gulosa* (Boisd.), also frequently defoliates *C. velutinus* locally in southern Idaho (Furniss and Knopf in press). Larvae of this moth are dispersed by wind; the female moth is essentially wingless. Outbreaks are generally terminated by a native virus but mortality occurs only in the later instars after feeding damage has occurred.

Damage done to seed by the eurytomid seed wasp, *Eurytoma squamosa* Bugbee can be a serious impediment to establishment of *C. martini* on deteriorated game ranges of Utah. Half of the seed crop grown for this purpose may be lost as a result of damage by this wasp.

Winter injury is one of the more striking forms of damage in the inland West. This appears to occur when ceanothus is subjected to unseasonably severe freezes in fall or early spring. Winter injury can be quite severe over large areas and it is fairly common to see whole hillsides of *C. velutinus* on which foliage has been freeze-killed.

Over extensive areas of the Inland Empire, Tarry and Shaw (1966) reported that *Ceanothus* spp. can suffer a late summer dieback for many years after freeze damage. They suggest that a severe freeze in November 1955 may have predisposed ceanothus to invasion by the root-rotting fungus *Armillaria mellea* (Vahl ex Fr.) Quél. This fungus disease is diagnosed by the presence of mycelial fans beneath the bark of roots, along with fungus rhizomorphs and a wet, spongy rot in dead roots. *A. mellea* probably spreads through clumps of ceanothus by a combination of root contacts and rhizomorph invasion. Once established, it might continue to spread locally for many years.

When diagnosing extensive foliage kill, it should also be remembered that ceanothus is quite sensitive to herbicides (Lyon and Mueggler 1968; Ryker 1970). Herbicide injury can be quite similar in appearance to winter injury. Thus, proper diagnosis requires knowledge of management practices as well as the weather record of a given area.

Cercocarpus

The foliage of mountain mahogany is available for browse throughout the winter despite heavy snowfall because of its height. The major immediate concern is that its stands are being excessively utilized by game and that the failure of regeneration in old stands has resulted in its foliage no longer being within reach of the game.

Broadly speaking, mountain mahogany appears to be relatively free of attack by insects and diseases. We do know of damage from sucking bugs (*Lecanium* sp. and others) and leaf diseases. We also know of two instances of severe infestation by the looper *Anacamptodes clivinaria profanata* (B. and McD.) and a bark beetle [*Chaetophloeus heterodoxus* (Casey)]. The looper infestation occurred in southwestern Idaho beginning in 1963 and lasted 3 successive years. One-half the stand covering several thousand acres was killed (Furniss and Barr 1967; Furniss 1971). A less extensive outbreak was reported recently on the Charles Sheldon Antelope Refuge in northwestern Nevada.

These outbreaks of the looper indicated that its destructiveness may be limited to pure stands that are dense and extensive. Also indicated was that the soil quality might limit survival of overwintering pupae beneath infested trees.

The bark beetle outbreak occurred during 1951 and 1952 in Oregon, where extensive stands of mountain mahogany were killed. This outbreak indicated that such infestation is common in branches or trunks of *Cercocarpus* weakened by other causes such as defoliation.

During the past 2 years we have noted the occurrence of a leafspot disease on mountain mahogany in many areas of Idaho, Montana, Nevada, and Utah. We are proceeding toward a positive identification of the causal fungus that appears not to have been previously recorded on mountain mahogany. This disease causes premature defoliation of old leaves, but damage probably is moderated by the development of new leaves.

Purshia

Bitterbrush [*Purshia tridentata* (Pursh) DC.] is found extensively in natural stands throughout the inland West, and is used for rehabilitating deteriorated ranges. It is frequented by greater kinds and numbers of insects (many of them beneficial) than any other shrub we have studied. To date, we have records of 80 insects and mites that infest bitterbrush, though most of them cause no conspicuous damage.

Several insects do affect the production of bitterbrush seed (Ferguson and others 1963; Basile and others 1964)--foremost among these being a thrips, *Frankliniella occidentalis* (Pergande); a midge, *Mayetiola* sp. (fig. 3); two gelechiid moths, *Filatima sperryi* Clarke and *Gelechia mandella* Busck.; and Say's stink bug, *Chlorachroa sayi* (Stäl) (fig. 4). Fortunately, bitterbrush produces seed prolifically and insects seldom take a critical toll. However, the Say's stink bug secretes a noxious fluid that might affect the palatability of bitterbrush plants. It might also migrate to cultivated fields, if nearby, and damage wheat and other grains.

Yields of bitterbrush browse can be reduced in areas of Idaho and Montana by leaf tiers (*G. mandella* and *F. sperryi*) that feed on the seed and foliage. Such infestations are easily detected in late summer from the brown appearance of the plants caused by partially eaten leaves adhering to the plants. Other defoliators include: the western tussock moth, *Orygia vetusta gulosa* (Boisd.); the tent caterpillar, *Malacosoma californicum* (Packard) (fig. 5), and the mountain mahogany looper, *Anacamptodes clivinaria profanata* (Barnes and McDunnough). For example, extensive defoliation and twig killing resulted when the western tussock moth infested bitterbrush near Reno, Nevada, during 1958-59 and again during 1963-64.

Figure 3.--Bitterbrush fruit infested by a midge, Mayetiola *sp. Larvae enter base of seed husk, killing the seed and resulting in a persistent, narrow-appearing fruit. Normal fruit drop to the ground in summer; infested fruit may remain over winter.*

Of grave concern is the severe dieback of bitterbrush on an estimated 30,000 acres of deer range in northern California and southern Oregon. The cause of this dieback has not been discerned, but there are several distinct possibilities. For instance, the eriophyid mite, *Aceria kraftella* K., causes symptoms like those reported. Also, juice sucking bugs, such as the bitterbrush tortoise scale (*Lecanium cerasifex* Fitch) (fig. 6), can cause branch dieback or possibly could be vectors or predisposers of disease. Numerous fungi have been cultured from the cankers associated with this dieback and six are possible pathogens (Calif. Forest Pest Action Council 1970). Apparently there is some indication that one or more of these fungi are responsible for this bitter-

Figure 4.--Say's stink bug, Chlorachroa sayi *(Stäl.) on bitterbrush. This bug damages seed.*

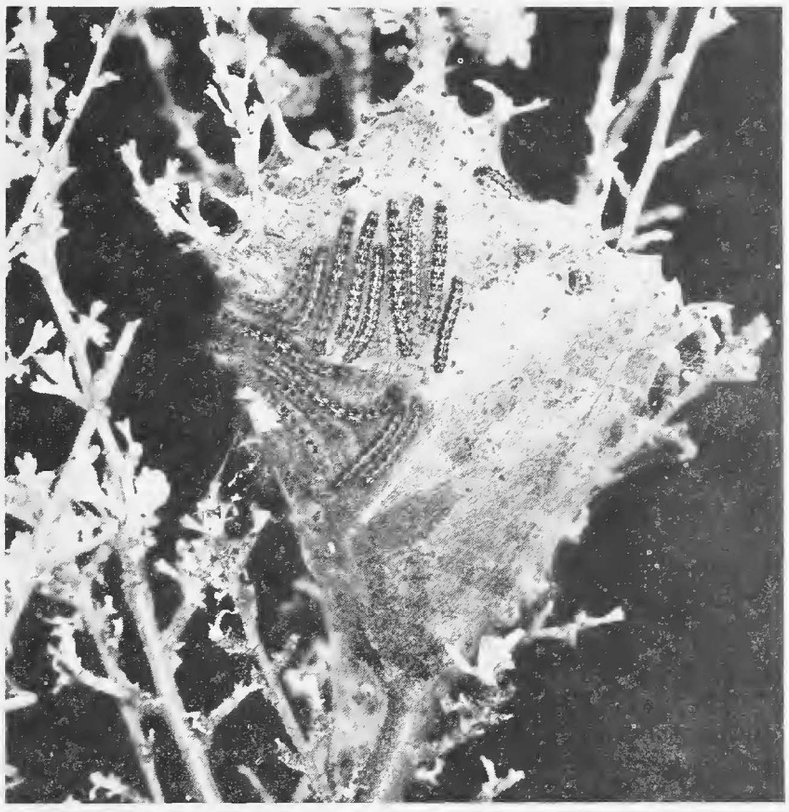

Figure 5.--Caterpillars of Malacosoma californicum *(Packard) on tent on bitterbrush. The caterpillars journey from their tent to feed on leaves.*

brush dieback (Calif. Div. Forest. 1969). Dr. R. Bega[1] is currently identifying these organisms and determining their capability to reproduce the dieback disease in bitterbrush. Also, physiological disturbances, such as winter injury, are known to cause bitterbrush dieback (Smith and others 1965) and could be at least a complicating factor.

A disease commonly encountered by biologists working with bitterbrush is damping-off of seedlings. There appears to be little natural resistance to damping-off (Peterson 1953) in bitterbrush, but disease intensity varies considerably with differences in soil and weather. Holmgren (1956) reported that mortality caused by damping-off ranged from none in 1951 to from 4 to 17 percent during 1952 in a planting area in Idaho. Brown and Martinsen (1959) attributed a portion of 16 percent mortality in a bitterbrush planting in Washington to such damping-off. Also, we wonder if part of their reported improvement in emergence of seedlings from seeds coated to discourage rodents might have resulted from the fungicidal effect of Arasan on preemergence damping-off organisms.

Both *Rhizoctonia solani* Kühn and *Pythium ultimum* Trow. have been implicated as pathogens capable of causing damping-off of bitterbrush (Nord 1965). These organisms probably could be controlled by fungicides. However, if fungicides are deemed as undesirable because of their possible side effects, research on techniques and timing of seeding or possibly, biological control using antagonistic fungi--might hold the key to prevention of losses by damping-off in seeding projects.

Salix

Willows are a prime source of winter browse for big game, especially moose. We have found 52 species of insects and 39 species of fungi that attack willows in Western United States. In addition, willows occasionally are parasitized by dodder (*Cuscuta* spp.) and mistletoes (*Phoradendron* spp.). Furthermore, sulphur dioxide seriously affects willows in local areas.

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[1]Personal communication from Dr. R. Bega, USDA Forest Serv., Pacific Southwest Forest and Range Exp. Sta., Berkeley, Calif.

Figure 6.--Female Lecanium cerasifex *Fitch attached to stems of bitterbrush. A similar scale infests mountain mahogany.*

Included among the native insects that can cause evident defoliation are buck moths, *Hemileuca* spp. and *Pseudohazis* spp.; a butterfly, *Nymphalis antiopa* L.; and the willow leaf flea beetle, *Altica ambiens* (LeC.). An introduced insect pest that is becoming increasingly common is the stem-infesting weevil, *Sternochetus lapathi* (L.). This weevil mines stems near the ground, thereby killing them by girdling or breakage (Harris and Coppel 1967). It was inadvertently brought into North America during the last century and is now widely distributed through much of the geographic range of willow. The oyster shell scale, thought to be another introduced pest, heavily infests some willows, resulting in branch killing and decadence of the plant.

Willows are also attacked by numerous diseases; the damage from some is quite devastating. Diseases that are caused by fungi, such as rusts, leaf blights, and cankers, are especially prevalent. The following factors apparently combine to favor spread and diversity of fungal pathogens: The common occurrence of willows in large continuous stands, the wide distribution and large number of willow species, and the moist habitats that willows normally occupy.

Besides the numerous fungal diseases affecting willows in the West, it is worthy to note an additional fungal disease that occurs close by because this disease probably could easily spread into Western United States, if it has not already done so. It is the willow scab and black canker disease, which is incited by *Pollaccia salciperda* (All. and Tub.) Arx [syn. *Fusicladium saliciperdum* (All. and Tub.) Tub.] and *Physalospora miyabeana* Fuk. This disease complex is thought to have been introduced into eastern North America from Europe. First reported in Connecticut, it was soon found killing many thousands of willows in the Eastern States and in Canada's Maritime Provinces (Davidson and Fowler 1967). In 1952, the two causal fungi were found on twig cankers of willow in the Fraser River Valley of British Columbia (Conners and others 1941). The perfect stage of the scab phase of this disease, *Venturia chlorospera* (Ces.) Karst., has been reported in Colorado (USDA, ARS 1960).

Figure 7.--Blister canker disease caused by Cryptomyces maximus *(Fr.) Rehm. on stems of willow in the Gros Ventre drainage of Wyoming.*

Another canker disease appears to be causing considerable mortality of willow shoots on elk and moose range of the Gros Ventre drainage in northwestern Wyoming.[2] This summer we found the perfect stage of the causal fungus, which we identified as *Cryptomyces maximus* (Fr.) Rehm. This disease has long been known in both Europe and North America, but probably not in the damaging proportions that we have here in the West (fig. 7).

Discussion

In reviewing various sources of information for this paper, we were impressed by how little attention had been focused upon insect and disease problems of wildland shrubs. Possibly, the only significant exception is a publication about diseases of wildlife habitat plants in Northeastern United States by Pearce and Spaulding (1942).

Many pests and disorders of shrubs usually persist in small numbers and seldom cause obvious damage. However, such pests can be quite influential in determining which plants continue to dominate sites because the success of shrubs often is dependent upon their competitive ability and life span. It can also be expected that manipulation of wildland plant cover at times will upset natural balances between plants and their pests, so that some seemingly innocuous pests become new and serious problems. Until we have considerably more information about the interaction of pests with shrubs in various environments, the safest strategy for wildland management is to favor a diversity of shrub species of local genetic origin. Imports probably should be used in large scale rehabilitation projects only after thorough local screening.

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[2]Personal communication with George Gruell, Wildlife Biologist, Teton National Forest, Jackson, Wyoming.

Obviously, insects and diseases must be considered in endeavors to genetically improve wildland shrubs. For instance, there is evidence from Plummer's planting site in Ephraim Canyon[3] that *Amelanchier* ecotypes vary in susceptibility to *Gymnosporangium* rusts. Some ecotypes showed very little infestation, and others were killed by the rust Thus, it appears promising to utilize resistant *Amelanchier* in browse rehabilitation projects.

The geographic ranges of diseases and insects are not static and introduction of pests can be devastating. The oyster shell scale, the willow borer, and willow scab-black canker are among the many pests that were introduced from Europe that are well established now in North America. Movement of native pests can also result in serious consequences. The western tussock moth appears to have bridged great distances to infest ceanothus in Idaho, apparently coming from California or western Nevada. Recognition of potential pests which might be introduced is an important problem and quarantines might prevent much grief. Movement of shrubs even for research should be carefully evaluated as they might inadvertently carry pests capable of dire consequences.

An increasingly disturbing factor is air pollution and its effects on wildland shrubs. Shrubs growing on wildlands close to smelters in the West have been damaged severely by fluoride and sulphur dioxide (Anderson 1966; Shaw 1952). Also, ozone appears to be particularly harmful to woody plants including several native shrubs (Noble 1965). Research is needed to determine if game might be harmed by eating shrubs affected by air pollution. Anderson (1966) and Wiese (1960) have pointed out that vegetation in the vicinity of a phosphate processing plant in southeastern Idaho contained levels of fluorine far higher than the 30 p.p.m. limit established by the National Research Council as being acceptable for livestock feed.

Wildland shrubs can serve as reservoirs of pathogens of serious economic consequence to agricultural crops. The Say's stink bug, which damages bitterbrush, also infests wheat and other small grains and drastically reduces their yields. Virus diseases are possibly of even more serious concern. Through much of the West, the wildland shrub, chokecherry, carries the Western X-disease, which is of grave concern to peach and cherry growers. As a safeguard against Western X-disease in orchards in Utah, Richards and Cochran (1956) advised: "...chokecherry should be brought under the noxious weed law and its use as an ornamental or as a conservation plant should be judiciously restricted."

Other Rosaceous shrubs, such as serviceberry, can harbor harmful viruses (Hilborn and others 1965) and should be carefully examined as possible reservoir hosts of orchard tree viruses. When agencies consider making extensive changes in vegetation on wildlands, they should carefully assess the risk of indirect consequences to other resources Before such an evaluation can properly be made, we need much more information on pest interactions.

In closing, we should not overlook the beneficial aspects of pests. Some insects and fungi that occasionally kill back old stems may actually benefit game by stimulating sprouting, thereby increasing the browse value of the plant. This might be particularly important with tree shrubs such as willows that might otherwise grow beyond the reach of game where fire is excluded. Insects and diseases also influence plant succession by changing species composition as a result of their specificity for certain plants. Hopefully, some insects or diseases may prove useful in reducing less desirable shrubs like ninebark [*Physocarpus malvaceus* (Greene) Kuntze] in favor of some others of greater browse value. This approach is being investigated in the Southwest (Ueckert and others 1971) where the twig girdler (*Onicideres rhodosticta* Bates) may help reduce the presence of mesquite (*Prosopis glandulosa* Torr.) and thereby favor grasslands. Biological control of some undesirable plants has proved feasible and is one of the more acceptable techniques of manipulating composition of vegetation.

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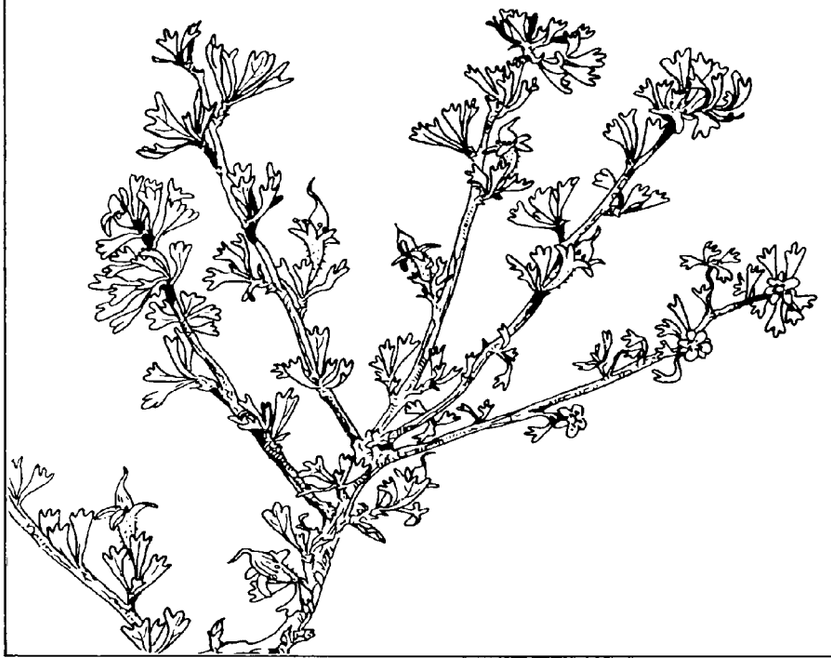
[3]Personal communication from A. Perry Plummer, USDA Forest Serv., Intermountain Forest and Range Exp. Sta., Ephraim, Utah.

Section V.

Physiology of Shrubs



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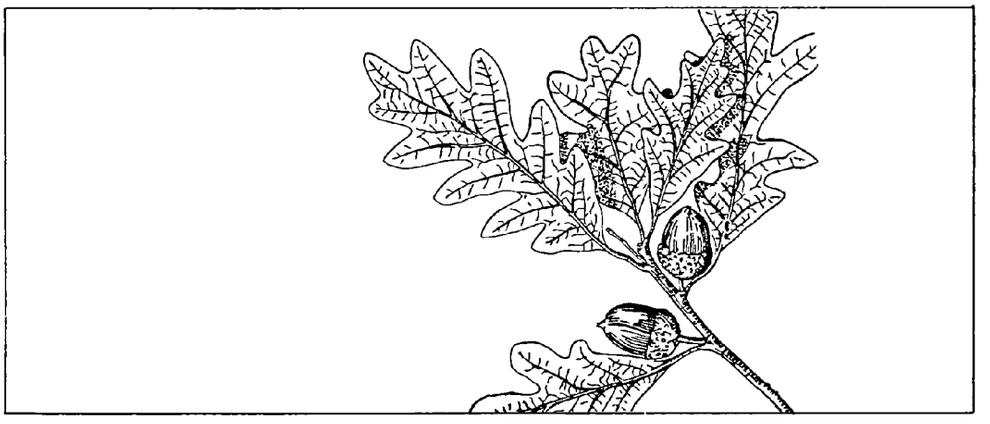

Physiology of water stress

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The water supply of wildland shrubs is a determining element in their habit of growth and their survival. Much work has been done to increase our knowledge of the way in which shrubs utilize water and respond to water scarcity and to wide variations in water supply. This paper describes some of the water relations of shrubs and the physiological and structural adaptations they have developed.

Effects of water supply on shrub distribution

Water supply plays a dominant role in controlling distribution of shrubs. This is shown dramatically by the high concentration of woody shrubs in small, ordinarily dry water courses of the Sonoran desert. Even though the amount of available water is low, it sustains growth of hardy woody shrubs. From a mountain viewpoint, the plains are crossed by numerous lines of shrubs and occasional trees; between these water courses are extensive barren areas (Jaeger 1955).

Mooney and Dunn (1970) showed that in the corresponding summer dry, winter wet, or Mediterranean-type climates of Chile and California, the plant communities were similar. In both areas, the dominant growth forms were the same at about the same position along a moisture gradient extending from 80 to 1,600 mm. annual rainfall. At the arid end of the gradient, rainfall was restricted to winter and spring.

An evergreen forest dominated at the wet end of the gradient at the highest latitudes. Toward the dry end of the gradient, the forest was replaced by dense evergreen shrubs, then by an open drought-deciduous scrub community, and finally by an open community composed of drought-deciduous shrubs as well as many succulents (Mooney and others 1970).

Plant cover and stature, as well as average leaf size of the evergreens, decreased with increasing aridity. The shrubby evergreen plants generally had extensive root systems, a long period of photosynthesis, but low capacity for photosynthesis (on a leaf-area basis about half of that of drought-deciduous plants). The drought-deciduous plants generally had shallow roots and high photosynthetic rates which prevailed for only short periods during the year. In regions of long periods of drought, the photosynthetic advantage of the evergreens decreased.

Because water supply controls establishment, survival, and productivity of shrubs of arid regions, the boundaries of steppes and deserts change frequently. Walton (1969) reported that in the 4-year low-precipitation period of 1944 to 1947 in Tunisia, the desert margin was 270 km. farther north than it was in the wetter 4-year period of 1931 to 1934. In 1947 even olive (*Olea*) trees at Sfax near the Mediterranean Coast dropped their leaves and many shallow-rooted plants were killed. Hence, in zones where rainfall is limited and widely variable in distribution, the boundaries between arid and semiarid areas are transition zones rather than lines marking abrupt changes in species or plant associations.

Efficiency of water use by shrubs of arid zones

Water use efficiency is generally measured as the "transpiration ratio" or "transpiration coefficient," the ratio of transpiration (T) to net photosynthesis (P). For plant communities it is usually the ratio of evapotranspiration to total dry matter produced. Under most conditions T/P varies from <200 to >2,000. High production crops or pasture plants have low values and plants of arid regions have high values. Maximum efficiencies can be expected only under optimal conditions for growth. Even with irrigated, high-production crops in ideal climates, however, transpiration ratios of about 100 prevail for only a few weeks during the year and the average ratio generally is considerably higher.

In arid regions, T/P values are very high (often in excess of 2,000) for two main reasons: (1) the leaf area index (area of leaf surface per unit area of ground surface) usually is between 1 and 2, so the rate of evapotranspiration is high in comparison to growth rate; and (2) the infrequent rainfall and extensive root systems are conducive to long periods of respiratory consumption of food reserves without high rates of photosynthesis. When precipitation does occur, the plants must photosynthesize with a restricted amount of leaf tissue. In addition, the steep vapor pressure gradient from leaf to air tends to increase T/P (Slatyer 1964).

Many xerophytic shrubs use considerable water and are not structurally adapted for low transpiration when water supplies are ample. The thick and small leaves of xerophytic shrubs have abundant stomata and well-developed palisade tissues. As shown by Turrell (1944), xeromorphic or sclerophyllous leaves usually have more cell wall surface exposed to the internal leaf atmosphere than do mesomorphic leaves. Hence, when stomata of desert shrubs are open and water supply is adequate, transpiration rates are high. However, because of their thick layer of cutin, such plants often have low cuticular transpiration when the stomates are closed.

Gindel (1971) grew *Eucalyptus gomocephala*, *E. camaldulensis*, and *E. occidentalis* plants under both high and low soil moisture regimes. In plants grown in water-deficient soil, leaf area was 31 to 43 percent smaller, and transpiration rate was from two to four times lower. However, when the soil was recharged with water to the same level for both groups, the group with the smaller leaf area showed an equal or higher transpiration rate.

A special class of water-wasting plants of arid regions are the phreatophytes (e.g., *Tamarix pentandra*, *Populus* spp., *Salix* spp., and *Prosopis* spp.), which line about 16 million acres of waterways throughout the Western United States. It has been estimated that these plants deplete nearly 25 million acre feet of water (McGinnies and others 1963). Blaney (1961) estimated that about half the water lost by *Tamarix* could be saved by replacing this plant with Bermuda grass in a 36-mile portion of the Pecos River channel in New Mexico.

Water deficits

The low available water supply results in the frequent development of water deficit in arid-land shrubs.

Characterization and measurement

The degree of water deficit of shrubs can be characterized in terms of water potential (Ψ); relative water content (RWC) which is synonymous with relative turgidity (RT); and saturation deficit (SD).

Water subjected to molecular restraints does not enter into physiological reactions within plants as readily as pure free water. Restraints may result from differences in

pressure, salt concentration, adsorption at colloidal interfaces, confinement in capillaries, or inadequate water supply at a particular place. Water potential (Ψ) is the difference between the free energy of water in a system and that of pure free water, the reference state, at the same temperature. Some of the forces affecting Ψ are:

1. Osmotic potential (Ψ_π). The osmotic component reduces the chemical free energy of a solution as a function of the presence of dissolved salts, sugars, and other solutes.

2. Matric potential (Ψ_m). The matric component reduces Ψ as a function of capillary or colloidal forces by soil colloids, cell colloids, and cell walls. The force of adsorption between the matrix surface and the water molecules reduces Ψ below that of pure free water.

3. Pressure potential (Ψ_p). The pressure component may increase or decrease Ψ depending on whether the molecules are subjected to pressures above or below atmospheric pressure. Under atmospheric pressure, the effect in an open system (e.g., soil) is zero. Turgor pressure in plants adds free energy to the system and Ψ is increased. At wilting, the pressure component approaches or reaches zero and does not appreciably influence Ψ.

In addition to Ψ_π, Ψ_m, and Ψ_p, temperature and gravity affect total Ψ.

Saturation deficit (SD) and relative water content (RWC) compare water content of plant tissue at a given time with water content of the same tissue when it is fully turgid.

Saturation deficit (SD) and relative water content (RWC) are calculated as follows:

$$SD(\%) = \frac{\text{saturated weight-original weight}}{\text{saturated weight-ovendry weight}} \times 100$$

$$RWC(\%) = \frac{\text{original fresh weight - dry weight}}{\text{fresh weight (fully turgid tissue) - dry weight}} \times 100$$

For a discussion of problems and sources of error in determining internal water deficits in plants, see Harms and McGregor (1962), Clausen and Kozlowski (1965), Barrs (1968), and Brown (1970).

Water transport and water deficits

The soil-plant-atmosphere system may be considered as a physical continuum through which water movement occurs along a path of decreasing potential energy. The driving force for water transport, then, is the decreasing energy gradient of water. The path of water transport includes movement in soil toward roots, absorption by roots, movement across root tissues into xylem elements and upward to the leaves, evaporation into the intercellular spaces of the leaves, and diffusion through the stomata into the external atmosphere.

There is resistance to flow throughout the soil-plant-air continuum (fig. 1). The resistance is greater in the soil than in the plant, and is maximal in the transition from the leaves to the atmosphere where water changes from liquid to vapor (Hillel 1971). In stems of woody plants, water transport occurs in the sapwood, and resistance in the heartwood is very great. In gymnosperms, this resistance occurs through sealing of pit pairs through aspiration, occlusion with extractives, incrustation of pits with ligno-complex substances, and combinations of these. In angiosperms, resistance is provided by tyloses in vessels and various extractives (Kozlowski 1968).

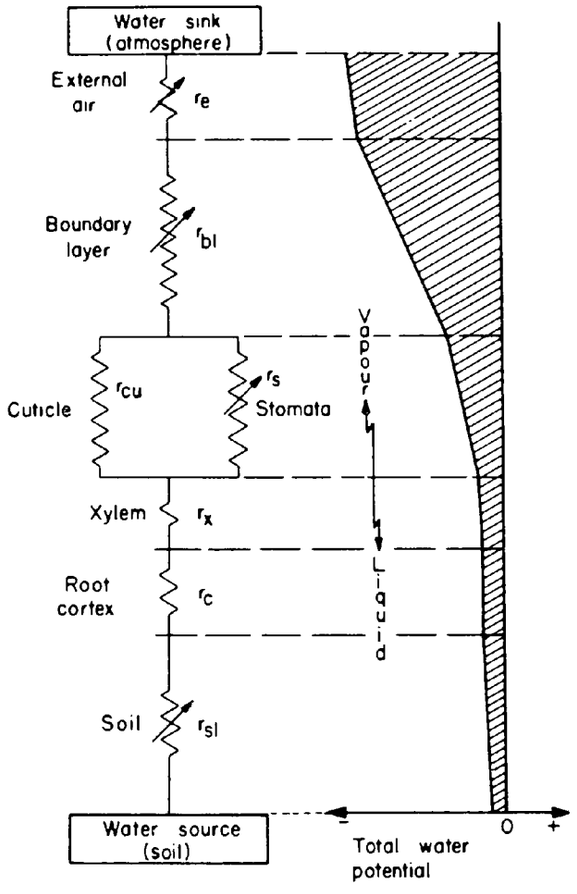

Figure 1.--An electrical analog representing resistances to the transpiration stream (From Rose 1966).

Upward translocation of water through the soil-plant-air continuum requires that Ψ_{plant} be lower than Ψ_{soil}, with the lowest Ψ in the leaves. Transpirational water loss from leaves of a plant growing in wet soil progressively reduces the soil water content and Ψ_{soil} (fig. 2). Associated with these changes is a reduction in Ψ_{plant} (and water content of the plant), resulting in an increased internal water deficit. Hence, on a day-to-day basis, there is an overall decline in Ψ of a plant growing in drying soil. Superimposed on this trend are diurnal variations in internal water balance of plants. Basically these are controlled by relative rates of absorption of water and transpirational losses. During the day, transpiration exceeds absorption. The resulting internal water deficits in plants are reduced or eliminated during the night, when both absorption and transpiration are low, but absorption is greater.

The graph shows changes in leaf water potential (Ψ_{leaf}), root surface water potential (Ψ_{root}), and soil mass water potential (Ψ_{soil}) as transpiration occurs over the 5-day period. During each day of the developing drought, transpirational water loss reduces Ψ_{leaf}, and because absorption does not keep pace with transpiration, the internal water deficit increases until absorption equals transpiration. The internal water deficit is reduced only when absorption exceeds transpiration. When the soil is wet, water flow is sustained by small differences in ($\Psi_{soil} - \Psi_{root}$). When transpiration declines late in the day and during the night, plant water content increases so $\Psi_{leaf} = \Psi_{root}$, and by early morning $\Psi_{leaf} = \Psi_{root} = \Psi_{soil}$. However, as Ψ_{soil} decreases (as during days 3 and 4) higher values of ($\Psi_{soil} - \Psi_{root}$) are needed to maintain flow because the hydraulic conductivity of the soil decreases rapidly. By the fourth day, some stomatal closure decreases flow. Nevertheless, equilibration of Ψ of the leaf, root, and soil occurs more slowly.

Wilting

As the water content and Ψ_{leaf} decrease, leaf turgor also declines during each succeeding day of a soil drying cycle, and a tendency to wilting becomes increasingly apparent. Wilting has been classified as incipient, temporary, and permanent (Kramer 1969). Incipient wilting, characterized by slight decrease of turgor, usually does not

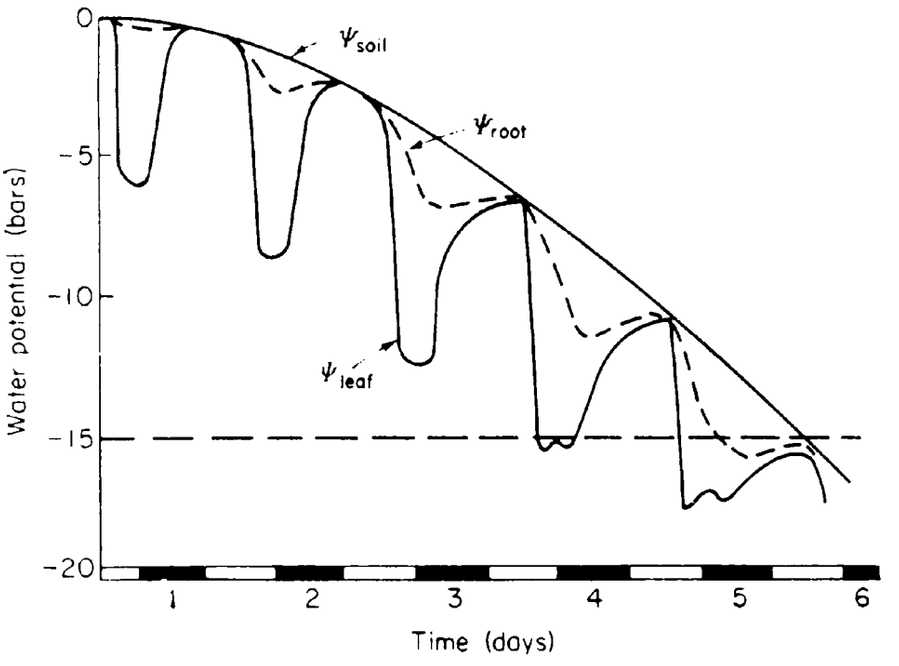

Figure 2.--Changes in leaf water potential (Ψ_{leaf}), root surface water potential (Ψ_{root}), and soil mass water potential (Ψ_{soil}) as water is lost from a plant initially growing in wet soil. The horizontal dashed line represents the Ψ_{leaf} at which wilting occurs. (From Slatyer 1967.)

cause drooping of leaves and occurs whenever conditions favor high transpiration rates. Incipient wilting grades into temporary wilting, with visible drooping of leaves during the day (when transpiration exceeds absorption) followed by rehydration and recovery during the night. During prolonged droughts, temporary wilting grades into permanent wilting, in which plants do not recover turgidity at night. Permanently wilted plants can recover turgidity only when water is added to the soil. In figure 2, if we assume that wilting occurs when Ψ_{leaf} reaches -15 bars, then on day 4 the plants would be wilted for several hours during the day, but would recover turgor during the night. By day 5, however, Ψ_{soil} also decreases to at least -15 bars. Therefore, on the night of day 5, Ψ_{leaf} would not recover sufficiently to establish positive turgor, since at the point when $\Psi_{leaf} = \Psi_{root} = \Psi_{soil}$, the Ψ would still be in excess of -15 bars. The plant would remain in a state of permanent wilting and would regain turgor only if the soil were irrigated.

According to Slatyer (1960b), permanent wilting occurs when $\Psi_{leaf} = \Psi_{root} = \Psi_{soil}$ and turgor pressure (TP) is zero. Gardner and Ehlig (1965) demonstrated, however, that symptoms of visible wilting in herbaceous plants appeared when TP dropped to between 2 and 3 bars. Hence, wilting was due to a change in elastic properties of the cell when TP declined below some critical value, rather than reaching 0. When TP exceeded 2 bars, leaf thickness was relatively constant and little flexing occurred with varying TP. When TP dropped below the critical value of near 2 bars, the elastic modulus declined markedly and the leaf sagged.

The relations between TP and visible wilting are complicated by variations in amounts of supporting tissues in leaves of different species. Some plants have leaves well supported by veins and show only mild wilting symptoms, whereas others have elastic leaves and show pronounced wilting when TP approaches zero (Gardner and Ehlig 1965). Rhododendrons are sensitive to drought conditions and their leaves curl before they yellow and turn brown during a drought. The leaves of *Syringa vulgaris* warp and wrinkle readily when under water stress. By comparison, the leaves of several species of *Ilex* and *Pinus*, which are well permeated with lignified tissue, do not droop readily even after they lose a great deal of water and TP is low. Some sclerophylls and halophytes do not show wilting symptoms even though they have severe water deficits.

Resistance of shrubs to desiccation

The ability of many shrubs to survive in extremely arid conditions is partly due to their resistance to extreme desiccation over long periods. The persistent and high degree of water deficit of desert plants is indicated by the observations of MacDougal (1936) on diameter changes of a palo verde *(Parkinsonia microphylla)* plant growing near Tucson, Arizona. Measurements were made at 2-week intervals from March 1929 through May 15, 1933. More than two-thirds of the 96 observations taken represented net stem shrinkages during each of the 2-week periods. Variations ranged from -0.45 to +0.35 mm. The stem increased in diameter following rain but thereafter it shrank again. Interestingly, the diameter of the stem was less on May 15, 1933, than it was in February 1929. Turner (1963) also showed that *Cercidium microphyllum* and *Olneya tesota* underwent severe internal water stresses during a spring drought in Arizona as reflected in their appreciable and prolonged stem shrinkage.

The capacity of desert shrubs to withstand extreme desiccation is also emphasized by the following recorded saturation deficits for plants of Palestine: *Artemisia monosperms*, 34 percent (April); *Atractylis serratuloides*, 47.6 percent; *Gymnocarpus fruticosum*, 52.6 percent; *Zygophyllum dumosum*, 57.8 percent (July); *Artemisia herba-alba*, 65 percent (August); *Helianthemum kahiricum*, 49.5 percent (September) (Zohary 1962).

Pronounced resistance to desiccation is particularly well illustrated by the studies of Slatyer (1960a, 1961) on *Acacia aneura* in central Australia. There *A. aneura* is one of the most valuable arid-zone plants because of its wide distribution and its high feed values. The individual trees are low and shrubby. The "leaves" are actually phyllodes about 1-3 mm. wide, 1 mm. thick, and 3-10 cm. long. The region in which *A. aneura* grows has sporadic rainfall. On occasion up to 90 percent of the rainfall is received in 2 months of the year, and often there is no rain for as long as 3 consecutive months. Hence, the plants persist under extreme aridity for long periods.

Using mature and immature *A. aneura* plants, Slatyer (1960a, 1961) compared water relations under weekly supplemental irrigation to eliminate severe water deficits and under natural field conditions. Measures included (1) phyllode water content as relative water content (RWC) determined by the methods of Weatherley (1950), (2) phyllode water potential obtained by the method of Slatyer (1958), and (3) osmotic potential of the cell sap (determined cryoscopically on expressed sap).

Evidence of extreme resistance of *A. aneura* tissue to desiccation is shown in figure 3. Severe water stress was required before the RWC of the tissue decreased to

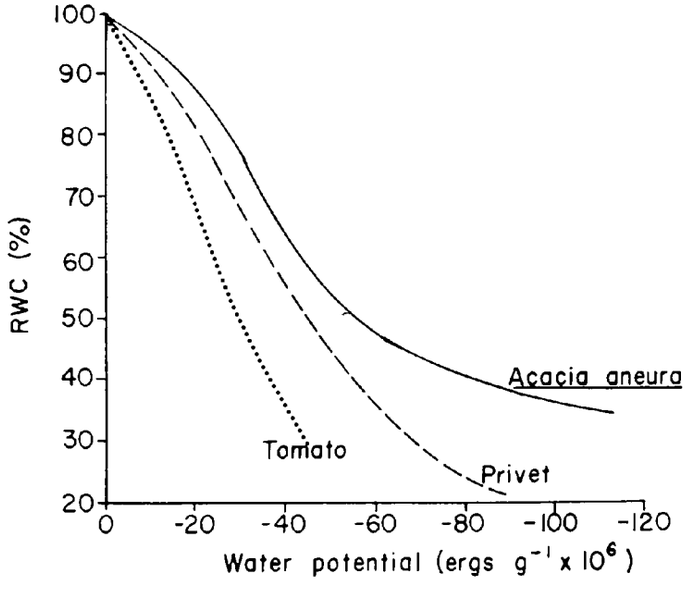

Figure 3.--Relation between relative water content (RWC) and water potential of Acacia aneura, *privet* (Ligustrum japonicum), *and tomato* (Lycopersicon esculentum). *(From Slatyer 1961.)*

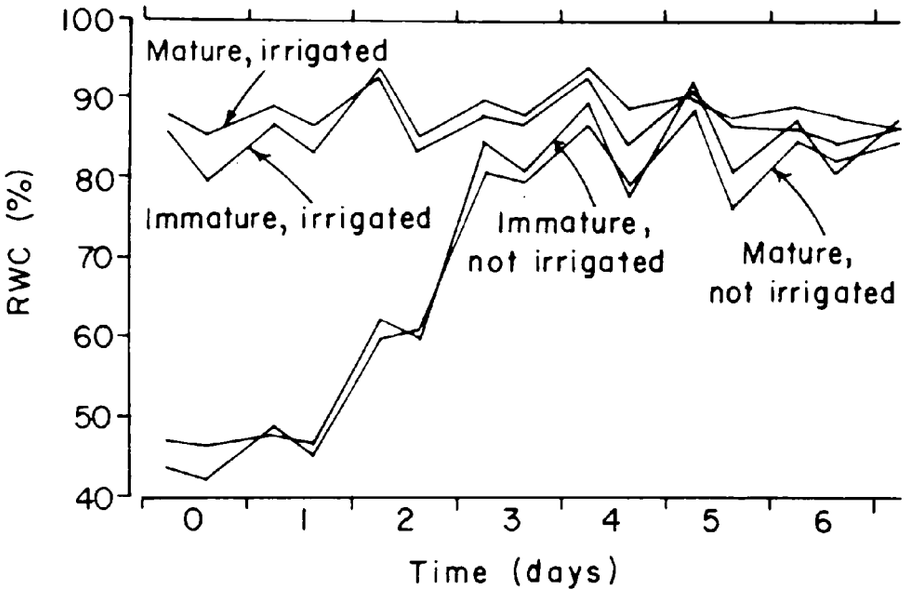

Figure 4.--Recovery of relative water content (RWC) after rain in irrigated and unirrigated Acacia aneura *plants. (From Slatyer 1961.)*

90 percent. A water potential of -15 × 10^6 ergs • $g.^{-1}$ reduced RWC to 92 percent and a water potential approaching -60 × 10^6 ergs • $g.^{-1}$ was required before RWC fell to 50 percent. The extreme resistance of *A. aneura* to desiccation is shown by comparison with two mesophytes, tomato *(Lycopersicon esculentum)* and privet *(Ligustrum lucidum)*. The end point of each curve represents the greatest desiccation to which the plants were subjected. In *A. aneura*, values of -130 × 10^6 ergs • $g.^{-1}$ could be tolerated but in tomato a value of only -5 × 10^6 ergs • $g.^{-1}$ caused death of the tissue.

Recovery behavior

Restoration of tissue hydration after rain shows the rate at which normal metabolism and growth are resumed. Figure 4 shows recovery of RWC after rain for both naturally watered and irrigated *A. aneura* plants. On the evening of day 1, 0.54 inch (13.5 mm.) of rain fell. RWC of irrigated plants reached maximum values by dawn on the morning after rain began (day 2). In naturally watered trees, however, uptake continued for 3-4 days before this stage was reached (day 4). Hence, the more severe the stress the slower was physiological recovery. Since 4 days were needed for recovery, most of the light rains that fell in the area did not result in resumption of normal physiological activity and growth. Increased growth could be expected only during the few times during the year that rainfall was heavy enough to promote soil water storage for periods in excess of 4 days.

The rate of change in RWC of naturally watered and irrigated plants following a rain is shown in figure 5. In irrigated plants, the RWC values remained high for 46 days after the rain. By comparison, RWC of naturally watered trees declined within a few days. Subsequently, a progressive decline continued until final RWC values of 30-40 percent were reached. There was also a diurnal fluctuation in RWC, with dawn and evening values higher than midday values. The younger trees showed a greater diurnal depression and more rapid recovery in RWC. All trees showed progressively less diurnal fluctuation and slower recovery of RWC as water deficits intensified. On days 4 and 11, a decrease of 20 percent was recorded during the day and almost full recovery was noted by 2200 hrs. On day 18, when soil water potential had been lowered greatly, only a small diurnal decrease in RWC occurred, indicating progressive stomatal control over transpiration. In the final phases of soil drying (soil water potential near minus 100 × 10^6 ergs • $g.^{-1}$), the very little diurnal fluctuation reflected effective stomatal control of transpiration and low cuticular transpiration.

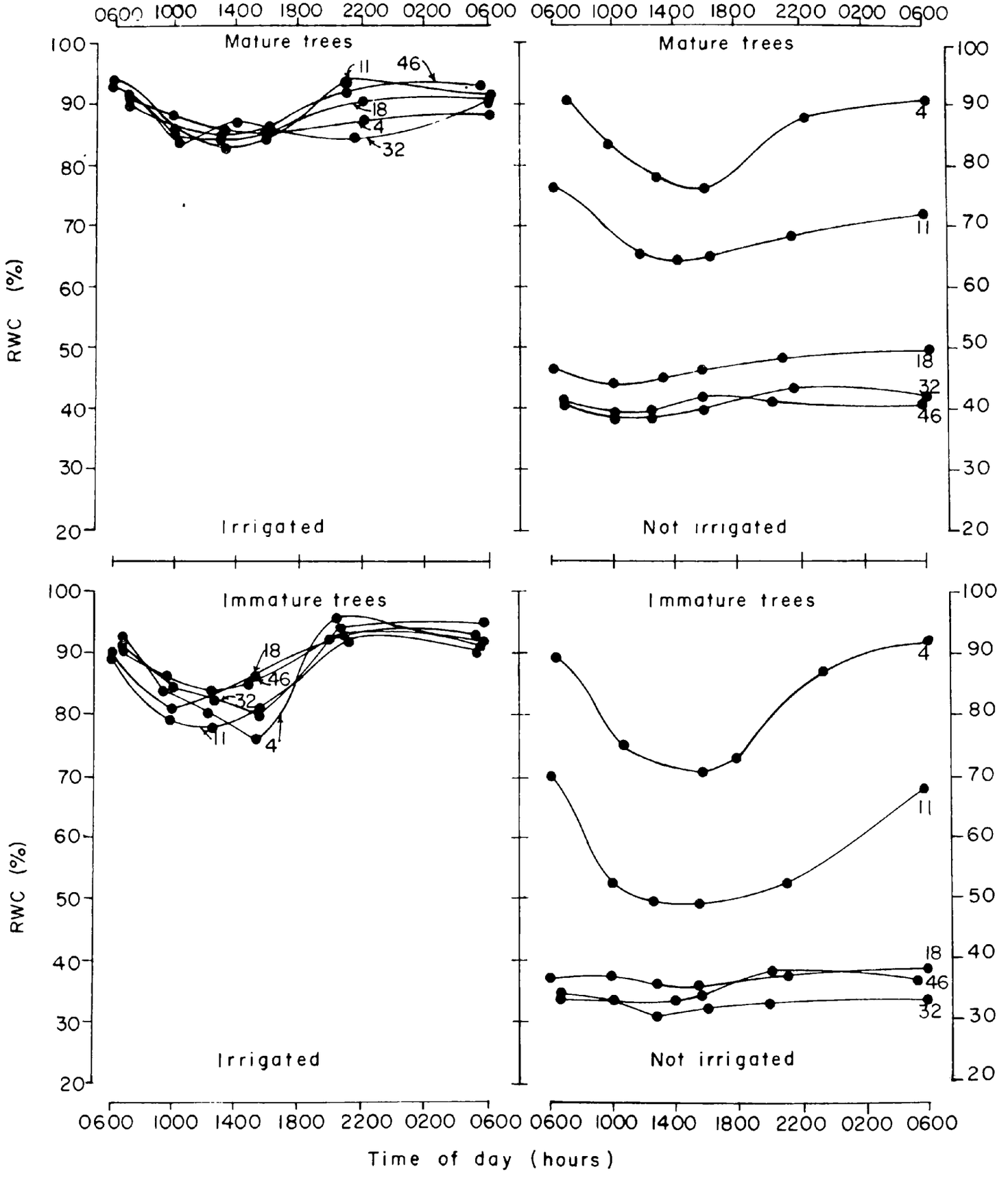

Figure 5.--Diurnal fluctuations in relative water content (RWC) of irrigated and unirrigated Acacia aneura *plants during an extended rainless period. Within each graph, each curve represents observations taken on the indicated day after the last rain. (From Slatyer 1961.)*

Role of atmospheric moisture in water balance

In arid regions, where neither rain nor ground water is adequate to sustain development of naturally occurring vegetation, atmospheric moisture in the form of dew and fog appears to contribute appreciably to the water economy of plants. In hot deserts, dew is common during the night, and because stomata of most species are closed at night, leaves must absorb water through the cuticle. Evaporation of dew from leaves may decrease transpiration in the morning. Also, the absorption of dew during the night may reduce the high internal water deficits which develop in leaves during the day (Slatyer 1960b).

The absorption of atmospheric moisture is particularly well known in the highly hygroscopic shoots of salt-secreting shrubs. For example, when wilted *Tamarix* plants were placed in a saturated atmosphere they rehydrated and regained turgor (Waisel 1960). Uptake of appreciable atmospheric moisture in plants that do not secrete salts has also been documented. For example, Waisel (1958) noted that during a prolonged drought in Jerusalem, dewed leaves of several species of shrubs and trees had a more favorable water balance early in the morning than undewed plants did. Experiments by Duvdevani (1964) in Israel showed that plants deprived of dew grew appreciably less than those receiving dew. In the United States, young *Pinus ponderosa* plants in very dry soil survived for 3 weeks, but when their needles were sprayed at night with a fine mist they survived for 7 weeks without additional watering of the soil (Stone 1957).

Went (1955a) described vigorous growth of shrubs in "fog deserts" (areas with little precipitation--about 1 inch per year--but frequent fogs) in southwestern Africa and along the coast of Peru. In these regions, fogs form as the air rises against mountains lying near the coast. In the coastal lowlands, where there is no fog, there is practically no vegetation. By contrast, at an altitude of about 1,000 feet, where fog hangs most of the year, a very lush shrubby vegetation is present. Atmospheric moisture may be utilized in arid regions.

Gindel (1965) showed that several xerophytic woody plants could be successfully planted during the rainless season in Israel if water from dew and mist was collected and concentrated in the root regions.

It has been suggested that in arid regions where humidity is high at night and the soil is very dry, water might move downward through the plant and possibly into the soil. However, Slatyer (1957) observed that when soil was very dry, water was absorbed from the air and accumulated in shoots. Although the diffusion gradient favored movement of water downward through the plant and into the soil, there was no evidence of such movement, presumably because of a discontinuity of contact between roots and soil. Vaadia and Waisel (1963) emphasized that xerophytes have thick cuticles and by their leaf structure they are less well adapted than mesophytes for rapid foliar absorption of water at night. Experiments with tritiated water confirmed that water not only entered leaves of plants but increased leaf hydration and probably contributed to plant survival. However, because of high cuticular resistance, entry of water into leaves was slow and its further downward translocation would depend on reversal of the usual water potential gradients. This would require a much longer time than the short period during the night when dew is absorbed by leaves.

Adaptations of shrubs for drought avoidance and tolerance

Many different features contribute to drought tolerance of shrubs. Survival is accomplished by varying degrees of desiccation tolerance and desiccation avoidance or postponement. Many shrubby xerophytes must also possess the capacity to survive and grow in the high salt concentrations of solonchaks or solonetz intrazonal soils. Such xerophytes have tolerance mechanisms to survive with high salt concentrations in the

cell sap. Some can exude salt or excrete high salt concentrations. Others avoid salt damage by regulating their life cycle to the restricted period during which the moisture content of the soil is high. Adaptation of shrubs to aridity consists in a combination of physiological and morphological features, which vary in degree among different species (Parker 1956, 1968). One outstanding adaptation (e.g., deep root penetration) may seem to predominate in insuring survival, or more than one structural or physiological feature may be effective. For example, creosotebush *(Larrea divaricata)* can survive long periods of dehydration by passing through low moisture periods in the vegetative stage. It also has wide-ranging roots so that it absorbs water from a large soil volume. When a drought continues for a long time, *Larrea* also loses its green leaves and keeps only the brownish ones.

Suppression of competing vegetation

Desert shrubs survive in part by their capacity to suppress development of competing vegetation. Chemicals released by the plant may inhibit germination and growth of competing plants, or the plant may monopolize the limited water supply. Inhibition of seed germination was shown in *Salvia mellifera*, which almost completely prevented establishment of *Adenostoma* seedlings under it (Went 1952). Naturally occurring growth inhibitors are widely distributed in tropical and subtropical vegetation. For example, fruits of *Ilex vomitoria* inhibited germination of seeds of *Prosopis juliflora* (Bovey and Diaz-Colon 1969). In arid and semiarid areas of India, *P. juliflora* forms dense thickets of small shrubs to large trees. Very few plants emerge within the community of these trees and shrubs, and a thick layer of leaf litter covers the ground. Inhibitors in the leaves affect seed germination as well as growth of shoots and roots of seedlings. Inhibition is enhanced by the physical effects of the leaf litter (Lahiri and Gaur 1969).

Naturally occurring allelopathic chemicals are released to the soil from both aerial tissues and roots of shrubs (Whittaker 1970) by leaching, volatilization, excretion, and exudation, and by decay, either directly or by means of micro-organisms. Among these chemicals are phenolic acids, coumarins and quinones, terpenes, essential oils, alkaloids, and organic cyanides. Chemical inhibitors of seed germination occur in all parts of fruits and seeds, such as the embryo, nucellus, testa, and pericarp.

Chemical inhibition may be difficult to distinguish from water restriction. Noting the regular spacing of *Larrea* plants in California deserts, some investigators have concluded that *Larrea* seedlings died in the vicinity of adult *Larrea* plants because of the toxic action of chemicals excreted by roots of adult plants (Went and Westergaard 1949; Went 1955b). However, Knipe and Herbel (1966) showed that root extracts of *Larrea* did not inhibit germination or growth of *Larrea* seedlings and were not detrimental to mature plants. Woodell, Mooney, and Hill (1969) attributed both the density and pattern of *Larrea divaricata* in California to soil moisture availability. At high rainfall levels, *Larrea* tended to be clumped; at low levels, it was much more regularly spaced.

The capacity of wildland shrubs to monopolize available soil moisture is shown by the effects of killing chaparral shrubs in California by hand weeding or herbicides (fig. 6). Where a dense cover of chaparral existed, very low soil water potentials were recorded. Only those species with deep root systems or ability to remain dormant for extended periods could survive in competition with chaparral in a region having prolonged droughts (McKell, Goodin, and Duncan 1969).

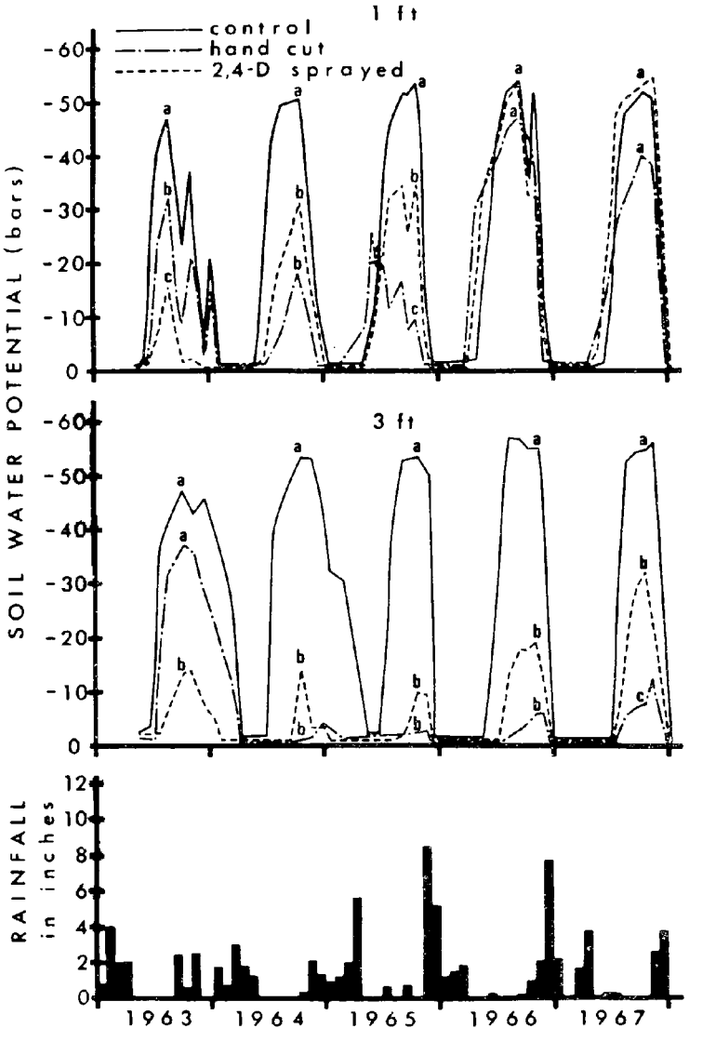

Figure 6.--Rainfall and soil water potential at 1 and 3 ft. soil depth under control, experimental plots in chaparral for 5 years. Plots were hand-cleared, sprayed with 2,4-D, or left as controls. Points indicated by the same letter on one date and depth do not differ significantly at the 5-percent level. (From McKell and others 1969.)

Leaf adaptations

The small size of leaves of desert plants is thought to be related to reduction in transpiration. Associated internal changes are increase in cell size, increase in cell wall thickness, development of a dense vascular system, high stomatal density, and proportionally greater development of palisade tissue than of spongy tissue. Although the volume of intercellular spaces is less in xeromorphic than in mesomorphic leaves, the ratio between the internal exposed surface area of the leaf and the external surface area is higher in xeromorphic leaves (Fahn 1964).

Shedding of Leaves and Shoots

If plants do not obtain enough water to balance unavoidable losses they often shed their leaves. Generally the shedding begins with the oldest leaves and progresses toward the apical meristems. During dry summers, shedding of old leaves occurs commonly even in the temperate zone. In the Mediterranean region, many deciduous trees and shrubs show much more premature defoliation than evergreens do. The large decrease in transpiration of these plants is correlated with seasonal changes in soil moisture availability. In the desert, leaves are often replaced by brachyblasts, reduced to stipules, or shed completely during the dormant season.

Leaf shedding during drought is well known in the ocotillo (*Fouquieria splendens*) of the southwestern United States; it drops its leaves during soil moisture depletion and grows a new crop several days after a rain. Four or five annual crops of leaves may occur in this species. *Encelia farinosa* of the North American deserts, and sometimes *Larrea tridentata* (McCleary 1968), also lose their leaves. Some leaf-shedding desert plants in Israel are *Artemisia*, *Noea*, *Haloxylon*, *Anabasis*, and *Zygophyllum*; Mediterranean plants include *Poterium spinosum*, *Cistus solvifolius*, *Thymus capitatus*, and *Artemisia monosperma*.

In Israel many plants are dimorphic and may have both long and short shoots. Seasonal dimorphism is attained by the shedding and growth of the different types of branches and leaves at different seasons. Large winter leaves are often replaced by small summer leaves. Orshan (1954) believes that reduction of leaf surface is the most important factor in water economy and survival of a variety of desert plants of the Near East. A number of desert and semidesert shrubs reduce the weight of their young shoots through abscission by amounts varying from one-third to more than three-fourths. Shrubs such as the "switch plant" (*Ephedra trifurca*) of New Mexico survive as leafless green twigs. Many plants of the great Indian semideserts (e.g., *Euphorbia royaleana*) also have no leaves (Sarup 1952).

Control of Stomatal Aperture

Transpirational loss from many plants is controlled by earlier stomatal closing during each day of a developing drought and by temporary stomatal closure during midday. The leaves of some sclerophyllous plants of arid zones have very effective structures for preventing both stomatal and cuticular transpiration. During extended droughts the stomata closed and transpiration was restricted to near zero in *Pinus halepensis, Laurus nobilis, Ceratonia siliqua, Arbutus andrachne, Rosmarinus officinalis, Citrus sinensis, Quercus palaestina, Pistacia, Olea europaea,* and *Cupressus sempervirens* (Oppenheimer 1947).

Shrubs apparently vary considerably in their capacity to close stomata during onset of drought. Stomata of plants of the Mediterranean maqui close rapidly when soil dries, whereas those of *Phillyrea media* do not (Oppenheimer 1953). Kaul and Kramer (1965) compared the drought tolerance of *Ilex cornuta* var. *Burfordii* and *Rhododendron poukhanensis* by measuring transpiration rates, water deficits, and stomatal aperture of plants during soil drying. Transpiration decreased faster in *Ilex* than in *Rhododendron.* Internal water deficits were higher in unwatered *Rhododendron* that in unwatered *Ilex* plants. Stomata closed sooner and at a smaller water deficit in *Ilex* than in *Rhododendron* when subjected to drought. *Ilex* appeared to be more drought resistant than *Rhododendron* because it controlled transpiration more efficiently and had a higher resistance to cuticular transpiration.

Quaraishi and Kramer (1970) reported that *Eucalyptus rostrata* seedlings were injured more during a drought than were seedlings of *E. polyanthemos* or *E. sideroxylon.* Transpiration decline curves for three species demonstrated that *E. rostrata* closed its stomates much later than *E. sideroxylon,* and *E. polyanthemos* was intermediate.

Stem adaptations

There is strong evidence that photosynthesis of branches and bark is an important adaptation to the arid environment. In the Sonoran desert, for example, several plants have rigid thorny branches and functional leaves are almost completely absent. Species include *Canotia holocantha, Holocantha emoryi, Koeberlinia spinosa,* and *Dalea spinosa.* In these plants photosynthesis occurs in the persistent stems and branches (Jaeger 1955). Branch and stem photosynthesis has also been well documented in drought-deciduous shrubs and trees. In Israel the young green branches of *Retama raetam* and *Calligonum comosum* carry on photosynthesis (Fahn 1964). Bark photosynthesis is very important in *Cercidium floridum,* which grows in the deserts of southwestern United States (Adams and others 1967; Adams and Strain 1969). This species, which has many small-diameter chlorophyllous branches, is leafless during much of the year. Adams and Strain (1969) compared field measurements of stem photosynthesis with those of leaf photosynthesis to estimate the relative contribution of each tissue to seasonal productivity of the species. During 1967 the stems contributed more than 40 percent of the total photosynthetic production of leafy trees. After a prolonged drought, leafless plants showed low rates of photosynthesis but these increased after autumn and winter rains. By midwinter, photosynthesis in a leafless plant was 86 percent as great as that in a plant

with leaves which grew in an area where it had not been subjected to extreme drought. Adams and Strain (1969) concluded that because of the high prevailing temperatures during the leafless period, bark photosynthesis probably was more important for *Cercidium* than for deciduous plants of other habitats.

Fahn (1964) suggested that the presence of living wood fibers containing reserve materials was another stem adaptation for survival during severe drought in Jerusalem. Living fibers were found in almost three-fourths of plants examined: in all species of Chenopodiaceae growing in the desert and in *Nitraria retusa, Gymnocarpus fruticosus, Achillea fragrantissima, Zillia spinosa,* and *Calligonum comosum* (Fahn and Leshem 1963).

Another adaptive character of desert shrubs is development of a wide cortex that protects vascular tissues from desiccation in early ontogeny and before development of periderm. Still another adaptive stem modification is development of interxylary cork. In *Artemisia cana,* interxylary cork forms early in the growing season as a sleeve over the previous year's xylem increment. The interxylary cork retards desiccation, especially near wounds, and restricts upward water transport to a narrow zone, thereby conserving water (Moss 1940). Interxylary periderm in *Epilobium angustifolium* also affords the plant protection against desiccation (Moss 1936).

Root adaptations

A highly efficient adaptation of desert shrubs is development of an extensive root system. This not only decreases water loss by exposing only a relatively small part of the plant to the atmosphere, but also provides high capacity for absorbing water from a large volume of soil. Because water in the soil not penetrated by roots is largely unavailable, those shrubs able to produce deeply penetrating and branching root systems use water most efficiently and prevent, or at least postpone, possible drought injury.

Within a single region may be found both plants with extensive but shallow roots and others with very deep roots and a few surface laterals. In Palestine some of the most important low desert shrubs have shallow root systems that spread horizontally in the upper soil, the only layer into which water penetrates. In deep saline soils of the Dead Sea region are shallow-rooted plants (e.g., *Suaeda palaestina, Salsola tetrandra* together with deep-rooting plants (*Prosopis farcta, Alhagi maurorum,* and *Suaeda monoica* (Zohary 1962).

Hellmers and others (1955) divided the rooting characteristics of chaparral plants of California into three distinct classes (figs. 7 and 8):

1. Woody shrubs with coarse major roots growing downward (e.g., *Adenostoma fasciculate, Arctostaphylos glandulosa, Ceanothus leucodermis, Photinia arbutifolia, Quercus chrysolepis,* and *Quercus dumosa).* Roots of *Adenostoma* and the two species of *Quercus* penetrated to a depth of 8 m.

2. Woody shrubs with coarse major roots with lateral growth exceeding the depth of penetration (e.g., *Arctostaphylos galuca, Ceanothus crassifolius, Ceanothus greggii* var. *vestitus, Ceanothus olignathus,* and *Cercocarpus betuloides*).

3. Subshrubs with fibrous root systems (e.g., *Diplacus longiflorus, Eridictyon crassifolium* var. *nigrescens, Eriogonum fasciculatum* var. *foliosum, Lotus scoparius, Salvia apiana, Salvia mellifera,* and *Yucca whipplei.* None of these species had roots that penetrated the soil deeper than 1.5 m.

Many shrubs exhibit deep root penetration in light soils where the water storing zone is deep. In savanna type vegetation in Brazil, several woody species including *Jacaranda decurrens, Attalea exigua,* and *Andira* spp. have roots that penetrate the soil at least 10 m. (Rawitscher and others 1943). Such plants lose water

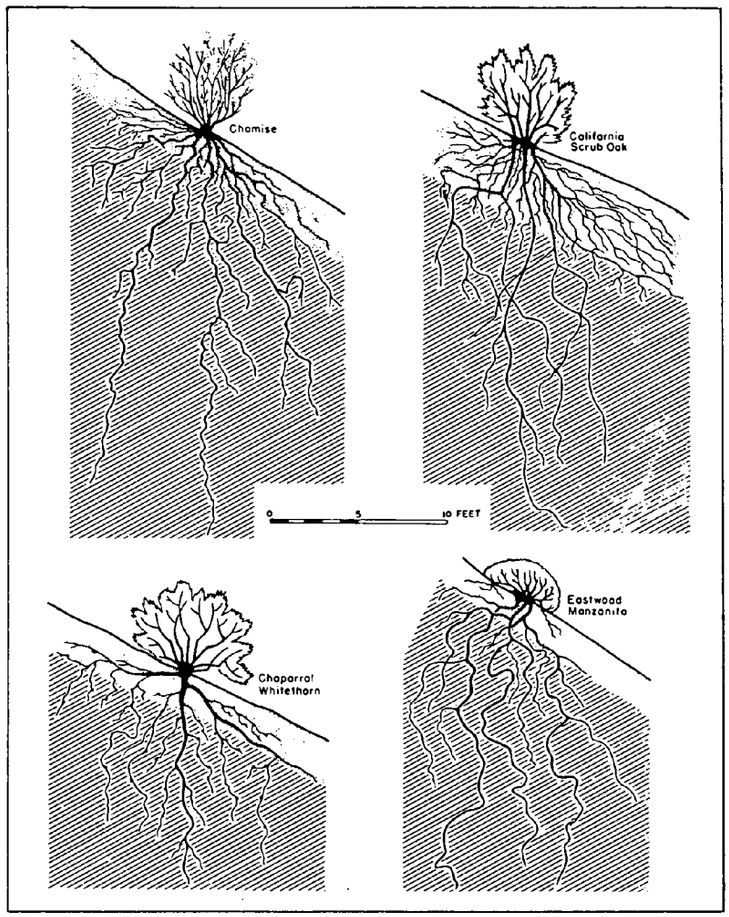

Figure 7.--Typical root systems of woody shrubs of California with deeply penetrating roots: chamise (Adenostoma fasciculatum), *California scrub oak* (Quercus dumosa), *chaparral whitethorn,* (Ceanothus leucodermis), *Eastwood manzanita* (Arctostaphylos glandulosa). *(From Hellmers and others 1955.)*

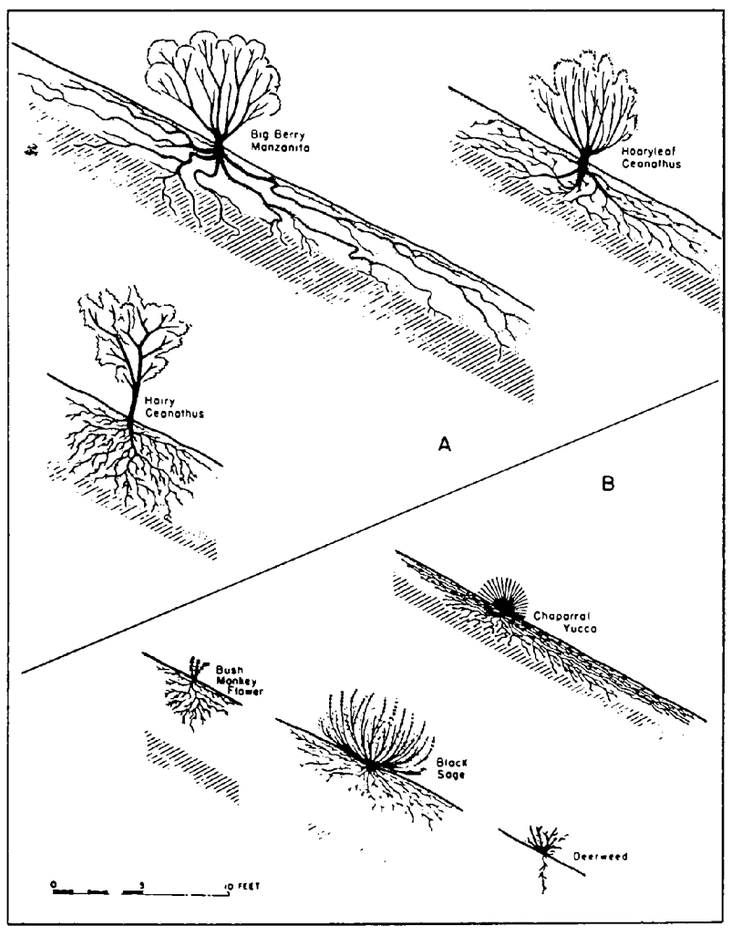

Figure 8.--Typical root systems of (A) woody shrubs with shallow roots: big berry manzanita (Arctostaphylos glauca), *hoaryleaf ceanothus* (Ceanothus crassifolius), *and hairy ceanothus* (Ceanothus oliganthus), *and (B) subshrubs with fibrous roots: chaparral yucca* (Yucca whipplei), *bush monkey flower* (Diplacus longiflorus), *Black sage* (Salvia mellifera), *and deerweed* (Lotus scoparius). *(From Hellmers and others 1955.)*

freely during the dry season, yet they do not undergo unusually severe internal water deficits. Herre (1954) reported that *Welwitschia mirabilis* roots grew downward to 18 m. in South African deserts.

Shmueli (1948) found that the deep roots of *Alhagi maurorum* and *Prosopis farcta* reached the fresh water table at a depth of 15 m. or more, and were not affected by salinity in the Dead Sea Area of Palestine, where salt content of the soil and dryness and temperature of the air are high. Because they had access to available water, the species listed (Shmueli 1948) in the following tabulation had high transpiration rates and developed internal water deficits during part of the year, especially at midday. This list of sample species shows length of time required to transpire water equivalent to the water content of the plant; these times are daily means within the period 0800-1700 hrs. for October 24.

Species	*Time (min.)*
Prosopis farcta	23
Alhagi maurorum	33
Nitraria spp.	130
Suaeda monoica	136
Arthrocnemum spp.	193
Suaeda fruticosa	240
Suaeda palaestina	390

In addition to having deep roots, these species reduced transpiration during certain hours of the day and they also shed their leaves periodically. Phillips (1963) also reported on very deep rooting (175 feet below the soil surface) of *Prosopis* near Tucson, Arizona. Kenesarina (1959) noted the well-developed root system of *Eleagnus angustifolia,* which survives the extreme aridity of Central Kazakhstan.

Often there are marked differences in rooting depth of various shrub species within the same genus. According to Krasilnikov (1960), the descending order of root penetration was *Euonymus europaea, E. maackii, E. hamiltoniana, E. yedoensis,* and *E. verrucosa.*

In heavy and hard soils of deserts, extensive flat rooting becomes the rule. Long horizontal roots (88 feet) were reported for *Prosopis spicigera* in the Great Indian Desert (Sarup 1952). The surface covered by the roots of a *Retama raetam* plant was at least 40 $m.^2$ (Evenari 1938), and 100-150 m. for bushes of *Larrea cuneifolia* and *L. divaricata* growing on the high plateaus of arid Argentina (Morello 1955).

As Oppenheimer noted (1960), several investigators found that survival of a number of shrubs and small trees of arid regions was due to root penetration of soft rocks of high water-holding capacity. In Israel, for example, where the covering soil layer dried out in summer, pine roots grew into soft limestone rocks. *Pistacia, lentiscus,* and *Quercus calliprinos* grew into and disintegrated rocks with the aid of excreted root acids.

Although deep-rooted species may be expected to have distinct advantages in drought avoidance over shallow-rooted species, in certain extreme environments they may not have access to more water than do shallow-rooted species. This was shown by Harvey and Mooney (1964), who studied seasonal growth characteristics, during an unusually dry year, of *Heteromeles arbutifolia,* a woody shrub with a deep penetrating root system, *Cercocarpus betuloides,* a woody shrub with a shallow, widespreading root system, and *Salvia apiana,* a subshrub with a shallow, fibrous root system. These chaparral shrubs were growing in the Mill Creek drainage of the San Bernardino Mountains at an elevation of 300 feet. From July 1960 to July 1961, the area received about 5.5 inches of precipitation, almost half in November. This amount of rainfall was far below normal. During

the previous season, 15.03 inches of rain were recorded and 20.33 inches during the year following the study year. During the entire period of study, soil water deficits were high. At a 12-inch depth, tensions were always near or greater than 15 atm.

Shoot growth of each species was negligible. The one exception was the slight growth shown by the shallow, fibrous-rooted *Salvia*. Presumably it used the small amounts of precipitation that penetrated upper levels of the soil profile. Adequate water apparently was not available during the period of study for growth of the more deeply rooted species. Nevertheless, the prolonged drought had no apparent subsequent effect on these species. In contrast to restricted growth of *Salvia* and essentially no measurable growth of *Cercocarpus* and *Heteromeles* during the drought year, vigorous growth was evident in all three species during the 1961-1962 season, emphasizing high resistance to desiccation ahd xerophytic adaptiveness.

When sands shift and dunes develop, some desert shrubs produce adventitious roots close to the surface where some soil moisture is available. For example, dune stabilization in New Mexico was aided in this way by such species as *Rhus trilobata*, *Poliomintha incana*, *Atriplex canescens*, *Populus wislizenii*, and *Yucca elata* (Shields 1961).

Roots of a few plant species are adapted for water storage. For example, *Ceiba parvifolia* of the Mexican thorn forest, where a short rainy season is followed by extreme drought, produces water-storing fleshy swellings or "camotes" in its roots, from which water is extracted for flowering and fruiting during the dry season (Moseley 1956).

Morphological and physiological plasticity in relation to drought

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Relative variability in annual rainfall (average deviation expressed as percentage of the mean) is generally understood to increase with aridity (Hershfield 1962, Katznelson 1964). In arid lands available water is the limiting factor for plant growth and development, and often even small deviations from the mean may prevent survival. Adaptations to variability in water supply are therefore important attributes of xerophytes. Such adaptations may be related to occasional variability caused by the irregularity in the scant rainfall of certain arid regions or to regular and seasonal variability in water supply as in the Mediterranean climate with its mild rainy winters and its long dry and hot summers.

These adaptations, whether structural or functional, are dynamic. They express the ability of xerophytes to adjust the size of the transpiring body and transpiration rates to the changing environment. Shantz (1927) recognized the importance of this ability in his classification of xerophytes into drought-escaping, drought-evading, drought-enduring, and drought-resisting plants. The system incorporates morphological and physiological adaptations to variability--mainly seasonal--in the amounts of water available to plants.

Among the plants persisting and remaining more or less active throughout the year, desert and Mediterranean chamaephytes are perhaps best adapted to seasonal and annual variability in available water.

I attempt here to sum up the available information on the adaptations of such plants in Israel and the neighboring countries.

Growth habits of chamaephytes

Chamaephytes were originally characterized by Raunkiaer (1907) as plants whose renewal buds are close to the ground; he later determined the buds to be not higher than about 25 cm. aboveground. He established four groups of such plants:

1. Half shrub chamaephytes (suffrutescent chamaephytes): aerial shoots orthotropic, more or less erect, not forming cushions.

2. Passive chamaephytes: aerial shoots orthotropic, but lying down on the ground because of their own weight.

3. Active chamaephytes: aerial shoots plagiotropic and prostrate.

4. Cushion plants.

Du Rietz (1931) distinguished between *holoxyles* (woody plants) and *hemixyles* (half shrubs) as the main life forms. He considers the maximal height of chamaephytes, either holoxyles or hemixyles, to be 80 cm. and not 25 as determined by Raunkiaer, arguing that 80 cm. is the limit between the shrub and dwarfshrub layers. Shrubs, according to Du Rietz, are holoxyles higher than 80 cm. and not developing a distinct main trunk with the stem branching from its basal part either above or below soil surface. Dwarf shrubs are holoxyles lower than 80 cm. Half shrubs, or hemixyles, are plants with only the lower parts of the epigeous stems lignified and perennial, and the upper parts herbaceous and annual. Du Rietz subdivided both shrubs and half shrubs according to height, growth form, and stem type. Shrubs are thus ctonophytic (growing on the ground), epiphytoidic, or parasitic. The ctonophytic are long-shoot shrubs (either erect or semiprostrate), or leafless succulent-stemmed shrubs. Ctonophytic dwarf shrubs are sedentary (i.e., without any rooting stems) or creeping (with prostrate epigeous rooting stems). The dwarfs are either erect or semiprostrate. The half shrubs or hemixyles are true half shrubs (suffraticose), or semiprostrate.

All these characteristics, although morphological by definition, are affected by lignification and by the relation between permanent and seasonal axis. These factors were considered by Schmid (1956) to be important in adaptations to environment.

Orshan (1953) tried to evaluate plant life forms with respect to drought resistance, and classified them according to the organs seasonally shed and the plant parts persisting throughout the year, and thus exposed to drought during the dry season. He distinguished four types:

1. Leaf shedders: plants seasonally shedding only the leaves and the inflorescence shoots.

2. Branch shedders: plants seasonally shedding parts of their branches.

3. Whole-shoot shedders: plants seasonally shedding the whole of their aboveground parts.

4. Annuals: whole plants that are seasonally renewed.

Plant parts that are shed seasonally are affected by the location of the renewal buds. However, these types cannot always be directly compared to Raunkiaer's life forms. For example, some phanerophytes are branch shedders. Raunkiaer's (1907) suffrutescent chamaephytes and Du Rietz's (1931) half shrubs correspond generally to the branch shedders, but these groups do not overlap exactly since branch shedding is not always directly related to lignification.

Adaptation by reduction of the water output

Reduction of the transpiring body

Many chamaephytes are seasonally dimorphic reducing their transpiring body during the dry season. This result is achieved in different ways in different plants (Orshan (1964). Generally it is related to plasticity in branch and leaf development.

On most chamaephytes, renewal buds appear late in spring at the end of the intensive growing season. From these develop small rosettelike brachyblasts, which may be either permanent or temporary. The permanent ones, such as some of those of *Poterium spinosum* and *Thymus capitatus* (Orshan 1964), remain short until they are shed. The temporary brachyblasts remain short during the dry summer only, start elongating at the beginning of the rainy season, and subsequently turn into dolichoblasts during the next spring (fig. 1). There is some morphological plasticity in that more brachyblasts become temporary under favorable conditions in plants like *Thymus capitatus, Thymbra spicata, Artemisia herba alba, A. monosperma,* and even *Poterium spinosum* and others.

Figure 1.--Thymbra spicata. *Left, an early summer aspect of a dolichoblast with the larger spring leaves, which start falling in an acropetal direction. At their axils new partial brachyblasts are being developed. Right, a partial brachyblast of last year bearing smaller summer leaves.*

The brachyblasts of certain species (e.g., *Teucrium polium*) do not remain short and rosettelike during the whole summer but soon start elongating very slowly. However, they do not develop into ordinary dolichoblasts (figs. 1,2). These have been called partial brachyblasts as opposed to absolute brachyblasts, which do not elongate at all. The leaves of the brachyblasts developed in summer are markedly smaller than those of the dolichoblasts developed in late summer and winter. Some dolichoblasts are heteroblastic, with leaf size and shape gradually changing in an acropetal direction,

Figure 2.--Teucrium polium. *The longer branches are dolichoblasts developed during the spring; they bear spring leaves with renewal buds at the axils. The shorter ones are partial brachyblasts.*

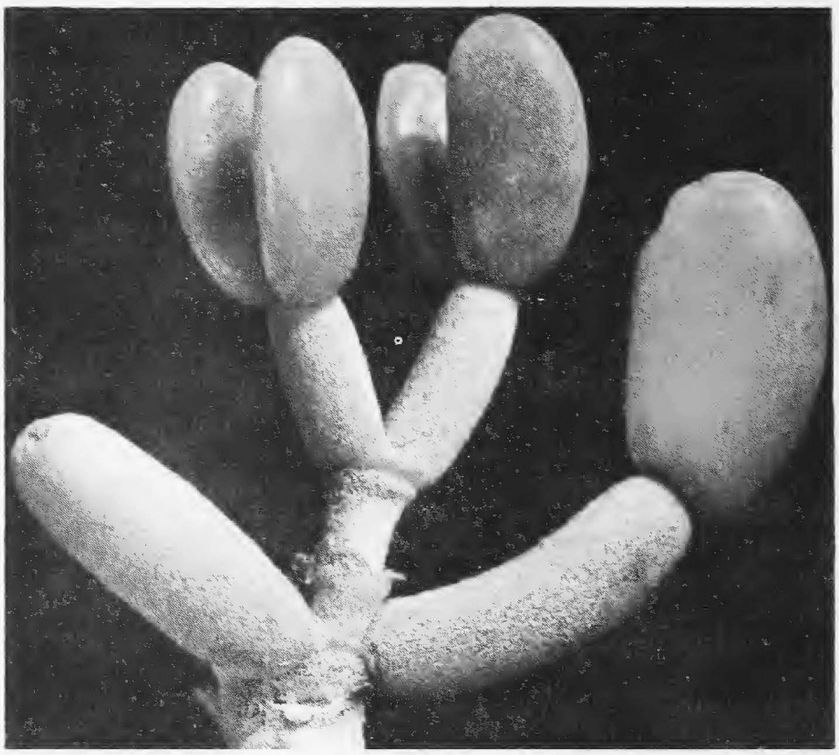

Figure 3.--Enlarged part of a Zygophyllum dumosum *branch. The upper leaves are with leaflets attached. The lower at the right side has one leaflet only, and the lower left has no leaflets.*

the lower leaves being larger and more differentiated morphologically (e.g., *Ononis natrix, Artemisia herba alba,* fig. 2).

The transpiring body is reduced by gradual leaf shedding during early summer. This shedding generally is also in an acropetal direction, so that by midsummer only the smaller leaves of the brachyblasts remain. A special case is *Zygophyllum dumosum* (fig. 3), the leaves of which are composed of a succulent petiole and two succulent leaflets located on top of it (Evenari and others 1971). At the beginning of summer the leaflets and later part of the petioles are gradually shed (fig. 4).

Figure 4.--Early summer aspect of a Zygophyllum dumosum *branch.*

Figure 5.--Poterium spinosum. Left, *spring dolichoblasts.* Right, *winter brachyblast terminating in an inflorescence bearing fruits.*

Detailed life cycles of selected plants are described in an earlier paper (Orshan 1964). Some example of diversity in branch morphology of certain species are shown in figures 5 through 7.

The relative reduction rate of the transpiring body is the decrease in weight of the transpiring body during summer expressed as a percentage of the maximal weight in spring. During 1957 and 1958, the range was from 45 to 75 percent for Mediterranean chamaephytes and from 70 to 96 percent for desert chamaephytes (Orshan and Zand 1962; Orshan 1964). These values were of approximately the same order of magnitude for 1957, when rainfall was 178 mm. in the desert stand and 621 mm. in the Mediterranean stand; and for 1958, with 32 mm. and 384 mm., respectively.

The spring weights of the transpiring bodies, on the other hand, were quite different for the 2 years. Weights of the desert plants in 1958 amounted only to 47-76 percent of the corresponding values for 1957, whereas weights of the Mediterranean chamaephytes were 85-107 percent. The latter values probably reflect a greater number of dolichoblasts in 1957 and a higher growth rate of these dolichoblasts. The higher values obtained for the Mediterranean chamaephytes in 1958 suggest that the 384 mm. of rainfall were not limiting the growth of the Mediterranean plants as 32 mm. were limiting growth of the desert plants. Moreover, the fact that relative seasonal body reduction for the same species was of the same order of magnitude in a bad and in a good year, and that the values for desert chamaephytes were higher than for Mediterranean ones, suggest that desert and Mediterranean plants differ from each other in some internal characteristics.

To find out to what extent ample irrigation affects the growth of some desert chamaephytes, plants growing in their natural habitat were compared by Evenari (Evenari and others 1971) in a good year (1964), when rainfall markedly exceeded the average,

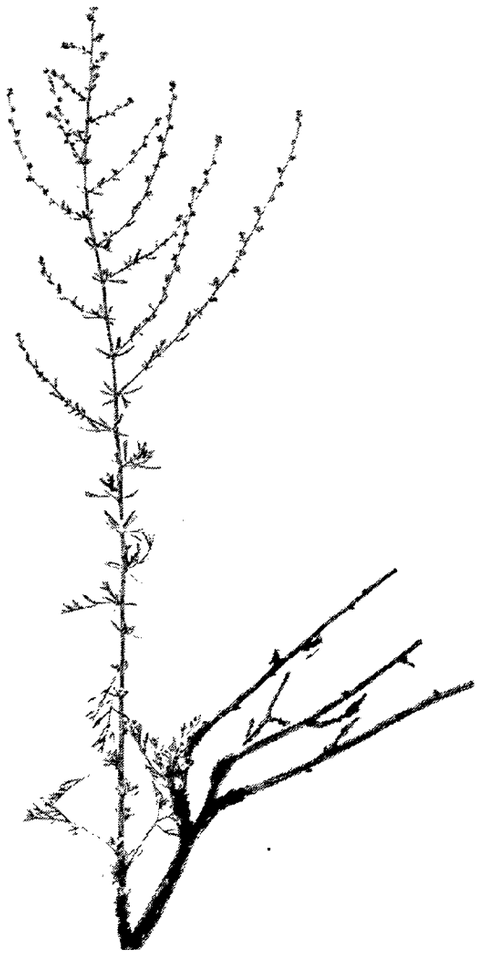

Figure 6.--A dolichoblast of Artemisia herba alba.

Figure 7.--Enlarged part of the branch shown in fig. 6. Note the larger spring leaves with absolute brachyblasts developed at their axils bearing much simpler and smaller leaves.

with irrigated plants growing under the same climatic and edaphic conditions. Lengths of the measured branches of unirrigated and irrigated plants (table 1) show that the effect of irrigation was more marked on *Zygophyllum* than on *Artemisia*, probably because most *Artemisia* branches are monopidial, ending with the inflorescence, and their elongation therefore comes to an end with the onset of flowering. Those of *Zygophyllum*, on the other hand, are sympodial and their elongation takes place from the bud below the apical flower. Under natural conditions both growth and flowering were affected by water supply only and not by photoperiod or temperature.

Reduction of the transpiration rates

Besides reducing their transpiring body, chamaephytes markedly reduce their transpiration rates during the dry summer (Evenari 1937; Evenari and others 1971; Orshan 1964). The relative reduction of transpiration rates ranges from 50 to 86 percent of the maximum values, but Mediterranean and desert chamaephytes do not seem to differ in this respect. The value for *Haloxylon articulatum*, 24 percent, is markedly lower than those of other plants measured. *Haloxylon* is an articulate chamaephyte and was measured in a sand-covered habitat.

Table 1.--*Effect of irrigation on branch elongation of four desert chamaephytes*

Plant	Branch length	
	Unirrigated	Irrigated
	Millimeters	
Artemisia herba alba	225	370
Reaumuria hirtella	115	210
Hammada scoparia	120	485
Zygophyllum dumosum	25	290

Water output in late summer

Reduction in transpiration rates interacts with surface reduction in reducing the water output of the plant. The water output of whole plants in late summer calculated as percentages of the maximal spring values was:

	Percent
Mediterranean plants (from Orshan)	
Poterium spinosum	18
Cistus salviafolium	12
Teucrium polium	19
Thymus capitatus	11
Desert sand dune plant (from Orshan)	
Artemisia monosperma	21
Desert plants measured in the Northern Negev (from Orshan)	
Artemisia herba alba	2.4
Zygophyllum dumosum	0.6
Noaea mucronata	2.2
Anabasis articulata	7.4
Haloxylon articulata	9.5
Desert plants measured in the Judaean desert (from Evenari)	
Retama roetam	1.8
Heliotropium rotundifolium	3.5
Haplophyllum tuberculatum	2.2

The values in this tabulation are strikingly small. However, those for the Mediterranean chamaephytes are markedly higher than those for the Northern Negev desert plants. Among the latter the articulate plants, *Anabasis articulata* and *Haloxylon articulatum*, show higher values than the nonarticulate ones. The values measured by Evenari for some chamaephytes of the Judaean deserts are of the same order of magnitude as those of the nonarticulate desert plants.

Other adaptations for survival

In years of exceptionally scant rainfall, when soil moisture available to plants has been almost exhausted, chamaephytes start dying in spite of their ability to reduce their water output so greatly. Death of these chamaephytes is peculiar; it is partial and takes place through dying out of radial sectors of the plant. The basis of this phenomenon is that most of the main branches are physiologically somewhat independent, each of them directly connected to a sector of the root system. In fact such a chamaephyte is a quasi-colony of independent functioning units (Ginzburg 1963; Evenari and others 1971). In time of stress these sectors compete with each other for the little water available to the roots and eventually some of them die. Their death increases the chances of survival of the remaining sectors.

The radial subdivision or splitting of chamaephytes occurs in different ways. The splitting of *Zygophyllum dumosum* is caused by discontinuities in cambial activity around the axis. Slowing and cessation of the cambial activity in longitudinal strips throughout the length of the axis separates each sector from its neighbors. They are held together only by dead tissue in the center (Ginzburg 1963).

Artemisia herba alba, aggregated rays in the secondary xylem undergo suberization and split the axis to several sectors. This normally occurs at the age of 4 to 6 years. In addition, a ring of interxalary cork develops at the end of each growth layer: this cork may serve as a protection and separation layer (Ginzburg 1963).

Another anatomical feature that might be related to survival is the presence of living libriform fibers and fiber tracheids which seem to be more common in chamaephytes (Fahn and Leshem 1963). Their exact role in survival is not yet known. They may be important in increasing the amount of "survival" water and reserve materials stored in the stems after the leaves have been shed, thereby increasing the chances of the stems to remain alive with a few dormant buds in time of stress.

Root system adaptation

Although root systems of desert plants have been studied by many authors (e.g., Cannon 1911, 1949; Evenari 1937; Kausch 1959; Tadmor and others 1962; Zohary 1962), their growth habits are by far less known than those of the shoots. Cannon (1949) attempted to classify root systems and relate them to their edaphic environment, but because roots are more plastic morphologically than shoots, and because their environment is more heterogeneous (soil, stones, rocks), it is often difficult to determine whether the root system of a certain plant belongs to one type or another. Therefore, a study was made of the root systems of chamaephytes growing in a sand-covered area in the 100-110 mm. rainfall belt of the Northern Negev of Israel (Gavish and Orshan 1972). It was hoped that in the relatively homogeneous sand layer the various root system types would be better expressed.

Three distinct types were determined, of which only one is equivalent to a type described by Cannon (1949). The root system of *Artemisia monosperma* is representative of the most common type found. Its well-distinguished vertical taproot runs to a considerable depth, and has three types of laterals:

1. Numerous annual horizontal laterals that are thin, shallow, and relatively short, and generally not deeper than 10-15 cm. These roots develop quickly immediately after the first rains and enable the plant to use efficiently any water penetrating the uppermost soil layers before it is lost by evaporation. They die during early summer.

2. Relatively few perennial laterals that are thicker, shallow, and long. They run horizontally to a certain distance from the taproot and then turn downward. They cover a wider area than the annual thin laterals and join them in using the soil moisture available in the upper soil layers.

3. A few deeper emerging laterals first descending obliquely and then turning more or less vertically downward. These roots insure survival of the plant during the summer when moisture in the upper soil layers has already been used. They penetrate soil layers deeper than those penetrated every year by rainwater. These lower layers are saturated occasionally in years with high rainfall, and water stored in them serves as a reserve. The density of the deeper penetrating roots is low. It seems likely that their growth is controlled by water available in the upper soil layers and is accelerated only under stress, resulting in penetration into soil volumes not used so far.

Most of the plants examined, i.e., *Retama roetam*, *Anabasis articulata*, *Haloxylon articulata*, *Thymelaea hirsuta*, *Echiochilon fruticosum* and *Moricandia nitens* belong to this type, which somewhat resembles Cannon's (1949) type VI cited as typical for xerophytes and common in sandy soils. However, he did not distinguish between two types of horizontal roots.

When plants like *Anabasis articulata* and *Haloxylon articulatum* grow on loessy soils that are not penetrated by rainwater to more than 50 cm., the whole root system changes and becomes shallow. However, if it is carefully examined, its three components are detectable. The taproot and its laterals run generally horizontally and the direction of growth and branching of the thick horizontal laterals are greatly affected by soil heterogeneity.

Fahn (1964) described an interesting anatomical adaptation of the roots of *Retama roetam* to desert conditions. He found that the anatomical structure of the long perennial horizontal roots was different from that of the vertical roots. The vessel elements of the secondary xylem of the horizontals are wider and longer than those of the verticals, and they increase with distance from the taproot. Fahn has suggested that the effect of this characteristic is to compensate for moisture stress by a much more pronounced decrease in suction pressure from the taproot toward the distal parts of the horizontal roots.

Origin of adaptations of chamaephytes

The morphological and physiological adaptations described above suggest a question: How did they evolve phylogenetically, and how are they affected by environment? Most authors (e.g., Bews 1927) suggest that chamaephytes were derived from phanerophytic shrubs, which were derived from trees. Zozulin (1968) suggests that half-shrub forms at least seem to have more than one origin. His tables show evolutionary trends leading to this growth form under arid conditions combined with either high or low temperatures.

Schmid (1963) suggested that the more primitive growth forms developed under tropical conditions were nonlignified perennial plants and that chamaephytes may have developed directly from nonlignified plants, perhaps under somewhat arid conditions. However, Schmid does not rule out the possibility that chamaephytes originated from trees through shrubs as an intermediary stage, especially under arid conditions, but he considers this development as secondary.

Meusel (1952, 1970) studied growth forms of selected genera with species distributed in Mediterranean and Central European habitats and related them to environmental conditions. For the genus *Carlina* he showed a transition from a branch shedding Canarian

and South Mediterranean small phanerophyte through small chamaephytes to Central European hemicryptophytes. This may be an adaptation to colder winters.

Environmental factors have a direct effect on the growth form of an individual plant. For *Ononis natrix* it has been shown that shading, and not soil moisture stress, had a marked effect on the change from winter leaves to summer leaves (Orshan 1938). *Poterium spinosum*, on the other hand, was not affected very much by shading, but its growth form was ultimately affected by photoperiod. The long dolichoblasts of this plant did not develop under short day conditions, and all branches remained as rosette-like brachyblasts. Under long days, on the other hand, branch elongation took place immediately, and all branches were spiny dolichoblasts resembling those developed under natural conditions during early summer (Berliner and Orshan 1971).

Discussion and conclusions

The data presented in this paper show clearly that desert and Mediterranean chamaephytes are highly plastic in their responses to a changing environment. The most important single parameter through which their water output is regulated and continuously adjusted to changes in the amount of available soil moisture seems usually to be the size of the transpiring body. Such changes are carried out through rapid growth when the plant is amply supplied with water and through gradual leaf shedding and branch dying-back when water supply to the root is limiting. The changes are brought about by various means in different species. Under Mediterranean climate they are related to season. Reduction of the transpiring body at the beginning of summer occurs through leaflet shedding in *Zygophyllum dumosum*, by dying out and eventual shedding of the green assimilating sheath of stems of articulate plants such as *Haloxylon articulatum* and *Anabasis articulata* (Evenari and others 1971; Fahn 1964), and by an acropetal leaf fall in many other chamaephytes.

Regrettably, little is known so far about the processes controlling growth and branch shedding. They seem to be affected by several factors apart from soil moisture tension and supply. Light intensity, photoperiod, and temperature seem to be important morphogenetic factors. For *Poterium spinosum* at least it has been demonstrated that photoperiod determines length and morphology of the developing branches (Berliner and Orshan 1971). Ample irrigation did not prevent leaf fall of *Artemisia herba alba*, *Ononis natrix*, and other plants during early summer when the plants were exposed to full sunlight.

A wide range is observable in transitions between brachyblasts and dolichoblasts, between absolute and partial brachyblasts and between temporary and permanent ones. Also, the size and morphology of the developing branches and leaves are determined by environmental conditions. These characteristics may be regarded as expressions of a certain plasticity of growth processes of chamaephytes. Physiological plasticity, expressed by partial death (in the ways lea fall and branch-shedding) and by the adjustment of transpiration rates, is the cause of morphological plasticity expressed in polymorphism of the chamaephytes' leaves and branches.

Although our knowledge of seasonal changes in the volume and shape of root systems is meager, we know that shallow annual horizontal roots develop in several desert chamaephytes. This points to the need for study of phenological changes in their root systems.

Physiology of salinity stress

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Inasmuch as more than 70 percent of the earth's surface is covered by water, it might seem that all of our water needs could easily be met for now and the future. But most, in fact almost all, of this water is salty. Between the extremes of sea water that may contain more than 35 milligrams per liter of dissolved solids, and pure water, our water resource is saline to brackish to sweet. As a direct resource, water from the ocean is unsuitable for agricultural, domestic, and most industrial use (van Hylckama 1971).

Fully one-third of the earth's land surface is arid or semiarid; much of its soil and water is too saline or alkaline for traditional agricultural production. Not all of these regions have always been salty; in some areas, natural surface flow of water carries dissolved salts to previously nonsaline soils. Ground water dissolves various substances from the soil and porous rock, including sulfuric acid from high sulfate clay, and calcium bicarbonate from reactions with limestone. Other substances, such as magnesium, sodium, potassium, iron, manganese, phosphorus, and silicon, are variously found in the rocks as carbonates, sulfates, nitrates, chlorides, bromides, fluorides, and iodides (Overman 1968). In arid lands, these geologic salt deposits are eroded; as a result, dissolved salts are spread over large areas. High rates of evaporation and low rates of leaching concentrate the salt in the upper soil and surface waters more rapidly than in regions of higher precipitation. The greatest single water quality problem in northwest Texas, for example, is the pollution of waters of the Brazos, Red, and Canadian Rivers by runoff and base flows containing high concentrations of dissolved minerals (Wells 1971).

Elaborate irrigation schemes throughout the world have contributed significantly to this relocation of salt. As supplies of high-quality water dwindle, the concentration process is accelerated, requiring larger quantities and more frequent "flushing" of the soil in order to leach out excessive soluble salts. Most agricultural crops cannot tolerate high quantities of salts in the soil. Thousands of irrigation water samples analyzed by the U.S. Salinity Laboratory have shown that poor quality of both surface and ground waters is a limiting factor in the success of irrigation in many areas (Richards 1954).

The salt cycle in arid environments

Shrubs are capable of cycling salts through the soil-plant system, and persistence of such plants is essential to the functioning of the ecosystem. Critically important plant nutrients, such as nitrates, occur as "islands of fertility" in arid regions (Garcia-Moya and McKell 1970). These are essential to the delicate balance of arid ecosystems, and any displacement of a species component will probably result in the loss of a particular nutrient through leaching. Once it is gone, there is little chance that nutrient input will coincide with establishment of a new plant (either the same or another species) to fill the niche.

High concentrations of soluble salts in the root medium affect plant growth in several ways. The total water potential at the root surface may be lowered, thus inhibiting water absorption by the roots; specific constituent ions in the saline media may induce toxicity or deficiency of one or more of the mineral elements in the plant; or there may be a combination of osmotic and specific ion effects (Hayward 1957). The problem of how soil salinity affects plant uptake and utilization of essential mineral elements can be extremely complex. Examples are sulfate-induced calcium deficiency in lettuce and calcium-induced potassium deficiency in carrots (Bernstein and Hayward 1958).

Osmotic inhibition of growth

Since different salts at equivalent osmotic potentials often produce equivalent growth depressions, the theory of osmotic inhibition has been well documented (Hayward and Long 1941). The reduction in growth under saline conditions is seen to be the lowering of the water potential at the root surface by the salts, thus resulting in a decrease in the water uptake by the plant (Hayward and Spurr 1944). Physiological drought caused by osmotic inhibition is difficult to distinguish from drought caused by a lack of water in the soil. In certain instances, they may represent the same phenomenon. The interactions of salinity and drought are complex. Even so, the theory of osmotic inhibition has been challenged by investigators who point out that plant cells maintain internal osmotic pressures sufficiently higher than that of the external medium to effect an adjustment that prevents osmotic loss of water to the medium (Bernstein 1961).

The total volume of water absorbed by a plant is affected not only by the rate of absorption, but also by the water-absorbing area of the root. Plants with shallow roots or with large top-to-root ratios show a low capacity for water absorption, and thus have poorer salt tolerance than plants with deep roots or those with low top-to-root ratios (Bernstein and Hayward 1958). A decrease in top-to-root ratio has been observed with increases in salinity (Bernstein and Pearson 1954). If osmotic adjustment occurs, the plant's absorbing capacity should not be impaired by the decrease, but osmotic adjustment does not always occur (Mozafar and Goodin 1970).

Specific ion effects

An element present in the soil in excess may cause metabolic derangements. It competes for entry with other elements present at lesser concentrations, and once absorbed, may inhibit enzymes, displace other essential elements from their normal, functional sites, precipitate other essential elements, disrupt the structure of water, and otherwise disturb plant metabolism (Epstein 1969). Actual concentrations need not be very high to produce some of these effects.

Research in the biochemistry of salt tolerance is scanty. Although the effects of salinity on specific metabolic reactions have long been postulated, experimental data are few. In alfalfa and tomatoes, Kling (1954) noted that the inhibition of growth with increases in salinity was accompanied by an increase in succulence and the production of darker green leaves. Boyer (1965) found a slow decline in net photosynthesis in cotton with salinity treatment. The stomata were reported to be open, and therefore the effect was attributed directly to salinity. Reports with many species indicate that a saline substrate increases respiration rates (Nieman 1962) and therefore specific enzyme systems associated with respiratory metabolism can be assumed to increase in activity. Such an increase would directly suppress growth by increasing the net assimilation rate (Slatyer 1967).

Very few ionic species occurring in soil solution or absorbed on the soil particles contribute to salinity in a given saline soil. The predominant cations and anions in soils are Ca^{++}, Na^{+}, Mg^{++}, Cl^{-}, $SO_4^{=}$, HCO_3^{-} and $Co_3^{=}$. Saline soils contain Na^{+}, Ca^{++}, and Mg^{++}, but of these cations, Na^{+} cannot exceed a given proportion if deterioration of soil structure is to be avoided (Richards 1954). High concentrations of Mg^{++}, for example, can be harmful to the plant, not only because they are toxic to the plant tissue but also because they can greatly reduce the absorption of Ca^{++} and K^{+} (Hayward and

Wadleigh 1949). If relatively high amounts of Ca^{++} accompany the Mg^{++}, this effect is usually avoided. High concentrations of Ca^{++} may produce nutritional imbalance, however, unless accompanied by some other cations such as Na^{+} or K^{+}. Van den Berg (1952) has suggested that salt tolerance is related inversely to the degree of calcium accumulation by the plant.

The specific ions likely to be most abundant and to cause the greatest problems are Na^{+} and Cl^{-}. Plant response to excess sodium may be complicated by indirect effects, such as structural deterioration of sodic soil with consequent poor growth of the plant because of restricted moisture transmission and seedling emergence. Direct effects of Na^{+} are its toxicity to sodium-sensitive crops and the change it imposes on the balance of nutrients in the relatively tolerant plants (Mozafar 1969).

Mechanisms of tolerance

Many studies have indicated that the tolerance of plants to chloride and sodium ions is associated with the relatively low rate of ion absorption (Greenway 1962). Because the primary discriminatory barrier to salt uptake appears to be in the roots, the xylem sap concentration of sodium and chloride ions may be very low, even though accumulation may be taking place in individual cells in the shoots (Scholander and others 1962).

Salts in large quantities in the plant cells have direct or indirect effects on protein hydration (Klotz 1958). This phenomenon may lead to the enhanced succulence observed under saline conditions in some species (Nieman 1962).

Changes have been reported in protein conformation and enzyme activities at low concentrations of sucrose or NaCl (Slatyer 1967). Similar effects may be induced by isosmotic substrates of different compositions (Gauch and Wadleigh 1944). These interactions take place at molecular levels, and therefore different results may be expected from, for example, K^{+} ions, which do not disturb the icelike structure of the hydration water of proteins, and Na^{+} ions, which do (Kavanau 1964). An excess accumulation of electrolytes in plant cells, especially of ions such as Na^{+} and Cl^{-}, can be expected to result in progressive changes in protein hydration and in enzyme activity (Slatyer 1967).

Plant species grown on saline media may regulate their ion uptake to a certain extent, but generally an increase in salinity causes an increase in ion uptake and a consequent buildup of salts in the plant organs. The excessive uptake of cations by the plant cells is commonly associated with an increase in the synthesis of organic acids (Jacobson and Ordin 1954). Sometimes the organic acid produced may not be favorable as far as food or forage value of the crop is concerned. Livestock intoxication by *Halogeton glomeratus* is attributed to this plant's excessive synthesis and accumulation of oxalic acid in response to excessive uptake of Na^{+} ions (Williams 1960).

Selective ion transport

In the salt economy of all plants--not only halophytes--selective ion transport is of utmost importance (Epstein 1969). It allows the plant to absorb from the environment essential nutrients in amounts conducive to growth and function; it regulates the flux of ions present in the external medium at high concentrations; and it helps to maintain internal osmotic pressures higher than those of the surroundings, and consequently, to maintain tissues in a hydrated state. Even though most crop plants cannot tolerate salt concentrations exceeding a few hundred parts per million, many halophytes can cope with concentrations up to and exceeding that of sea water (Rains and Epstein 1967).

Biological membranes are capable of transporting ions against concentration and electrical potential gradients. The necessary energy for this transport is believed to be furnished by metabolism (Epstein 1965). Ion transport across these membranes for

long periods of time can result in a much greater concentration of ions within the cells then in the solution bathing the cells (Sutcliffe 1962). A proposed mechanism of selective ion transport across a membrane which is impermeable to free ions is the "carrier concept" (Epstein and Hagen 1951).

Long - distance transport

Long-distance transport of ions is also important in higher plants. After the initial absorption by root hairs and cortical cells, ions are eventually delivered into the conducting system and make their way through the xylem to the top of the plant. After delivery to the extracellular spaces of the leaves, they become absorbed by the leaf cells. At this stage, ions have undergone two cellular transport processes. There is ample evidence in the literature that salinity in many species exerts its most damaging effect on the metabolism of leaf tissue (Gauch and Wadleigh 1944). Studies of long-distance transport to the leaf of the ions commonly found under saline conditions are therefore included in this paper.

Atriplex: a case study

Many taxa of the family Chenopodiaceae are indigenous to arid and saline regions of the world. Their adaptation to such an environment has interested many researchers. Shrubby halophytes of the genus *Atriplex* are particularly adapted to such conditions.

Atriplex plants are characteristic of those facultative halophytes that achieve salt tolerance by accumulating ions against a concentration gradient, and then "partition" those ions in specific cells. In *Tamarix*, salt glands, an anatomically distinct group of cells, concentrate the salt and then secrete salt crystals to the outside of the leaf surface (Thomson and Liu 1967). In *Atriplex*, the accumulation is accomplished by vesiculated hairs (trichomes) on the epidermis of both upper and lower leaf surfaces, and to a lesser extent on petioles and stems. As the salt concentration inside the hair reaches some critical level, the vesicle breaks and spreads its contents over the leaf surface. Crystals of salt form immediately, and over a period of time quite a litter of crystals and cell debris is built up on the leaf surface. Many *Atriplex* species provide high-protein forage for livestock and wildlife, and in *A. polycarpa*, for example salt accumulations on the surface of the leaf may become so great as to render the tissues unpalatable until rainfall washes the salt back to the soil surface.

Atriplex halimus, a Mediterranean species, lends itself to solution culture, as do most of the other saltbush species. Growth is greatly stimulated by low levels of salinity, and plants growing on different strengths of Roagland solutions achieved maximum growth at less than -1.0 atm. external osmotic potential (Mozafar, Goodin, and Oertli 1970a). Maximum dry-matter accumulation of plants treated with either NaCl or KCl occurred at -1.8 atm. osmotic potential. However, if NaCl and KCl were present in equimolar concentrations, maximum growth occurred at -4.4 atm. of external osmotic potential. These results suggest a more complicated growth phenomenon than simply an osmotic inhibition. The final mature size of the leaves was not affected by salinity treatments, and a comparison of fresh weight with dry weight shows that succulence is not a major contributing factor in salt tolerance for this species. Also, Na^+ absorption was not inhibited, as it is in most plants, by high concentrations of K^+ in the culture solution. On the other hand, K^+ absorption was greatly reduced by excess Na^+ in the medium. If the two were present at equimolar concentrations, Na^+ uptake was twice as great as K^+ (Mozafar, Goodin, and Oertli 1970b). Such data suggest a biochemical interaction only operative at high concentrations. It is not clear why *Atriplex* and other salt accumulators have low selectivity for K^+ in preference to Na^+ (Greenway and Osmond 1970).

Since osmotic adjustment fails to occur in leaf mesophyll of *Atriplex*, the excess salts absorbed by the root system must pass the ions on to the vesiculated hairs

(Mozafar and Goodin 1970). The concentration of salts in the vesiculated hairs of *A. halimus* was measured and found to be remarkably higher than that of the leaf sap and xylem exudate. Growing the plants under saline conditions increased the salt content of the hairs from 2.3 M $Na^+ + K^+$ to 11.6 M, but salt concentration of the leaf sap did not change appreciably.

We have also looked at the concentration of anions, primarily Cl^- and oxalate, and the calculated molarity of Cl^- increases sharply as salt concentration of the substrate increases. There is essentially no increase in oxalate synthesis (or accumulation), however, as a result of salinity increase. This finding is in contrast to that reported by Osmond (1963) for some Australian species of *Atriplex*. If the molarities for both anion sources are added, and compared with Na^+ and K^+ molarities, ionic balance is essentially achieved.

This plant reportedly fixes CO_2 by the C_4-pathway of carbon reduction, and there is a clear difference in the size and internal structure of the chloroplasts (West 1970). Osmond (1963) has reported that $^{36}Cl^-$ is accumulated in the hairs against a concentration gradient, and the accumulation is greatly stimulated in the light. He has noted that the rather high concentration of mitochondria would be typical of the high respiratory activity of a stalk cell; also, plasmodesmata connect the stalk cell to both the vesicle and the epidermis. We have also seen these plasmodesmata, and this is the likely means of transport across the cell wall.

Outlook for the future

We have grown several species of *Atriplex* under routine agronomic conditions as a forage crop (Goodin and McKell 1970). The yields are often as great as that of alfalfa, and the species could be adapted to arid regions where too little water is available for irrigation, or where the water quality is so poor that traditional forage crops cannot be grown. Solution culture experiments with *A. polycarpa* (Chatterton 1970) have shown that species to tolerate 39,000 p.p.m. NaCl and 80 p.p.m. boron. Such crops might be grown and harvested simply to remove excess salts and thereby reclaim land too saline for agricultural production.

Boyko (1966) has described field experiments in which he utilized saline water for the irrigation of crops. Through many years of experience he concluded that sustained productivity is possible under such conditions, provided certain ecological and hydrological principles are observed. Quick percolation of the irrigation water was found essential, followed by good aeration of the soil. Such conditions imply the need for a light, sandy soil or gravel. Boyko contends that the large, noncapillary air spaces in a coarse soil provide a chamber for only partial root contact of absorbing roots. Following percolation, the air space becomes a humid chamber and "subterranean dew" forms on the roots, supplying them with fresh water. This scheme would imply that absorbing roots are constantly being subjected to drastic changes in solute potential at the soil-root interface. Thus, species with exceptional drought and/or salinity tolerance would show a good adaptability to fluctuations in solute potential. In nature, most sudden changes would be in the direction of decreased salinity caused by rainfall. The change back to the formerly higher salt content would be a relatively slow process and more or less parallel to evaporation.

The demand for food for a hungry world requires that we seek every opportunity to increase production. We believe that the arid and semiarid regions offer one approach to that increase. By taking advantage of biological technology and innovation, we can develop new crops and new uses for old crops. Our goals must include reclamation of saline and alkali regions, and expansion into arid regions never before cropped. Through better understanding of the natural history, ecology, and physiology of the vegetation of these regions, the forgotten shrubs may make a major contribution to productivity.

Gas exchange of shrubs

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The integrated result of many physical and physiological responses of the plant to its environment can be neatly summarized in the measurements of net CO_2 and H_2O vapor fluxes. Attempts to relate gas exchange of individual plant leaves or branches to the productivity and water loss of plant communities are still in the early stages and fraught with difficulties (Larcher 1969; Ledig 1969; Jones, Hodgkinson, and Rixon 1969; and Botkin, Woodwell, and Tempel 1970). Nevertheless, measurements of photosynthesis, respiration, and transpiration yield a wealth of information on the inherent capacity of plant physiological processes as governed by both extrinsic and plant factors. In the first category are irradiation intensity, temperature, moisture stress, and humidity of the air; in the second, species and varieties, leaf types and ages, and phenological status. This review will consider the inherent photosynthetic capacities of various shrub species and the adaptive strategies they employ to maintain sufficient rates of CO_2 fixation to thrive in their particular environment. Concomitant rates of water loss through transpiration will also be taken into account.

Sources of variation in gas exchange patterns

There is much variation in gas exchange patterns. Rates of net photosynthesis, dark respiration, and transpiration per unit plant material can easily differ considerably between shrub species when measurements are made under similar environmental conditions. Widely distributed shrubs also exhibit intraspecific differences in gas exchange capacities. In addition, seasonal and diel patterns of photosynthesis and transpiration vary between shrub species. Shrub responses to stress are also exhibited in widely differing patterns of gas exchange.

Species differences

For several arid and semiarid shrub species, Hellmuth (1971) carefully detailed rates and patterns of CO_2 and water vapor exchange in the field. Under both optimal and moisture stress conditions, net photosynthetic rates closely paralleled transpiration activity. In agreement with the work of Stocker (1960) and Lange and others (1969), he found that all of these arid and semiarid species maintain positive net CO_2 gain during any 24-hour period, even under severe water-stress conditions. The only exceptions were very young and senescent leaves of *Rhagodia baccata*, which occasionally exhibited negative daily CO_2 balances. Maximum net photosynthetic rates varied by a factor of 10 between these different species. Under both optimal and water-stress conditions the trend was that semisucculent, glabrous, and mesomorphic species tended to have much higher daily CO_2 uptake values than sclerophyllous species. This is in agreement with the work of Mooney and Dunn (1970) who found much higher maximum photosynthetic rates in drought-deciduous shrubs than in sclerophyllous evergreen shrubs in the Mediterranean climates of California. Both shrub types possessed approximately equivalent average annual carbon fixation capacities, however. Obviously the sclerophyllous evergreen shrubs have adopted a strategy very different from that of the drought-deciduous shrubs to exist through periods of severe drought.

Hellmuth (1971) found no apparent relationship between dark respiration rates and the type of shrub. Daily net CO_2 gain on a 24-hour basis in semisucculent and mesomorphic species was found to be much higher, however, than in the sclerophyllous shrubs. The ratio of daily net photosynthesis to night respiration was also higher. Maximum transpiration rates and daily transpiration totals varied substantially among species, but there was no correlation with regard to a particular leaf type.

The water use efficiency--that is, the water vapor transpired for a 24-hour period divided by the net CO_2 uptake for the same period of time--was much more favorable in semisucculent and mesomorphic species than in sclerophyllous shrubs under reasonably optimal conditions. Under stress conditions there seemed to be no relation between water-use efficiency and leaf type. Mooney (1969) found that in two species of Mediterranean sclerophyllous evergreen shrubs subjected to water stress, dark respiration rates were much higher than in winter-deciduous shrub species. The evergreen species originated in warmer and drier areas and were obviously better adapted to conserve energy during periods of desiccation. This is in agreement with the studies of Larcher (1960) in Italy, who found that the evergreen Mediterranean *Quercus ilex* had lower gas exchange rates and was able to curtail water loss more efficiently under drought conditions than the deciduous *Q. pubescens*.

Environmental differences

A comparison of rates of dark respiration for shrub species at several elevations in the White Mountains of California (Mooney and others 1964) demonstrated that with increasing elevation shrub species had much higher dark respiration rates. Determinations of ratio of photosynthesis to dark respiration reflected this increased dark respiration rate with increasing elevation. Plants from higher elevations had much smaller ratios. In agreement with this, Klikoff (1966) found that mitochondrial oxidative rates from three herbaceous species also reflected this trend. Plants taken from higher elevations exhibited higher oxidative rates at 20° and 30° C. Higher respiration rates in plants from higher elevations and also from northerly latitudes has long been interpreted as an adaptive characteristic (Mooney and Billings 1961). Although high mitochondrial respiration rates may be necessary in cooler environments, low ratios of net photosynthesis to dark respiration would seem to be disadvantageous in terms of overall CO_2 gain.

Investigating transpiration rates in several shrub species in the White Mountains of California, Mooney and others (1968) found no correlation between the elevation of origin and the intensity of transpiration. It was clear, however, that summer-deciduous shrubs in the desert zones had particularly high rates of transpiration during active growth periods. Evergreen desert shrubs, however, had much lower transpiration rates even through times of high evaporative stress. Similarly, at high elevations evergreen shrubs had lower transpiration rates than did deciduous shrubs. This is parallel to the above-mentioned differences in gas exchange rates between evergreen sclerophyllous shrubs and drought-deciduous shrubs from the Mediterranean climates of California and Italy and the desert climates of western Australia.

Acclimation

The variation in gas exchange characteristics with environmental pretreatment can also be substantial. Sun and shade leaves of the same woody plants are well known to differ in both morphology and gas exchange capacity (Tranquillini 1955; Pisek and Winkler 1959). Similarly, the temperature regime to which plants have been exposed is known to influence absolute rates of photosynthesis and the relative response of net photosynthesis to different temperatures (Semikhatova 1960; Pisek and Winkler 1959).

Mooney and West (1964) demonstrated that a definite photosynthetic acclimation could take place within 3 weeks in several shrub species. These were first raised in

a greenhouse and then placed in gardens at several elevations in the White Mountains of California. Acclimation was expressed in the average rates of net photosynthesis and dark respiration, and also in the response of net photosynthesis to different temperatures. It was hypothesized that species with the widest natural distribution also exhibited the greatest degree of plasticity in terms of photosynthetic acclimation. As might be expected, species acclimated in the cooler environments exhibited optimal net photosynthetic activity at cooler temperatures whereas those plants acclimated in the warm desert environment had maximal net photosynthetic rates at higher temperatures.

Strain and Chase (1966) demonstrated similar acclimation tendencies in four desert shrub species following short-term acclimation at different temperatures in growth chambers. Following high temperature acclimation it was also apparent that dark respiration rates were reduced at higher temperatures. The plot of slopes for dark respiration as a function of temperature remained constant, however, indicating that the Q_{10} values had not changed. Only one species, *Chilopsis linearis*, showed reduced photosynthesis at high temperatures following high temperature acclimation. The optimal temperatures for net photosynthesis in the three other shrubs shifted several degrees, suggesting a truly adaptive plasticity as demonstrated for the species studied by Mooney and West (1964).

Seasonal conditions

Since acclimation can be accomplished in a few weeks, it is not surprising that gas exchange characteristics of shrub species vary considerably with the season. Strain (1969) carried out field measurements of summer and winter photosynthetic and dark respiration rates of some of the same desert shrubs investigated earlier in the laboratory (Strain and Chase 1966). *Larrea divaricata*, the most widely distributed species, displayed remarkably similar net photosynthetic rates in January and July despite different prevailing temperature conditions, suggesting that the plant had undergone a substantial degree of acclimation. This corroborated the earlier findings in the laboratory. *Hymenoclea salsola* and *Encelia farinosa* had shown a much narrower range of acclimation to temperature in the laboratory and, as might be expected, displayed widely differing net photosynthetic rates in January and July. All of these shrub species underwent a reduction in respiration rate with acclimation to summertime conditions, as observed by Mooney and West (1964).

Detailed ecophysiological studies of *Rhagodia baccata* and *Acacia craspedocarpa* by Hellmuth (1968, 1969) documented substantial seasonal change in absolute rate of net photosynthesis per unit plant material. Both species underwent light saturation of net photosynthesis at reasonably low light intensities (1,000 ft.-c.). Above saturating light intensities, in these species, net photosynthesis was strongly dependent on leaf temperature. During the year, however, the temperature optimum for net photosynthesis of *Rhagodia baccata* shifted from 30° to 37° C. (Hellmuth 1968). For *Acacia craspedocarpa* there was only a 2.5° C. shift (Hellmuth 1969). In both species, Q_{10} values for the net photosynthesis-temperature relationship changed somewhat during the year.

In a more recent study, Hellmuth (1971) investigated the gas exchange characteristics of several other western Australian shrubs under optimal soil moisture conditions in winter or spring and then under moisture stress during the late summer. There seemed to be little seasonal change in the optimum temperature for photosynthesis or the upper and lower thermal compensation points for net photosynthesis. In some species the light compensation points and saturation intensities for net photosynthesis were achieved at somewhat higher light intensities in late summer than in winter or spring. In several species, however, there was no change in light intensity values. All species saturated at surprisingly low intensities between 10 and 20 Klux.

A striking degree of seasonal change in the net photosynthesis response to temperature has been recently demonstrated by White, Moore, and Caldwell (unpublished data)

for *Atriplex confertifolia* in the cold deserts of northern Utah, where annual temperature extremes can easily extend from -30° C. to 40° C. Optimal temperatures for net photosynthesis shifted 10° to 20° C. between the spring and summertime. *Atriplex confertifolia* was found to carry on active photosynthesis when leaf temperatures were -5° C. in the early spring and also in the summer months at leaf temperatures in excess of 50° C. This degree of plasticity in photosynthetic acclimation to temperature exceeds that reported for other higher plants.

Seasonal acclimation of various shrub species might be at least partially explained by changes in the age or type of photosynthetic tissue, as indicated by Professor Orshan in this Symposium. In *Acacia craspedocarpa*, Hellmuth (1969) found that the mature green phyllodes in early summer differed noticeably in gas exchange functions from the yellowish phyllodes characteristic of the plant in late summer and early winter. The temperature optimum for net photosynthesis of green phyllodes was 35° C. whereas that of yellow phyllodes was 37.5° C.; the Q_{10} values for net photosynthesis and respiration and the absolute rates of CO_2 gas exchange also varied between the two types.

Because leaves of various ages are present during most times of the year on *Rhagodia baccata*, gas exchange characteristics as a function of leaf age could be easily tested in this species (Hellmuth 1971). During optimal moisture conditions in the winter or spring, the daily net photosynthesis was greatest in young leaves, intermediate in mature leaves, and least in very young leaves. Under moisture stress conditions in late summer, the series was somewhat altered in that mature leaves had the greatest photosynthetic rates, followed by young, very young, and finally senescent leaves, which had the least positive CO_2 fixation. Cardinal temperatures for net photosynthesis also varied with leaf age. Rates of dark respiration measured at 20° C. indicated that very young leaves had the highest rates, followed by young and then mature leaves. This same basic pattern held when the plants were under optimal water conditions or water stress. In water use efficiency of photosynthesis, very young leaves were lowest, followed by mature, then young leaves under optimal soil moisture conditions. Under stress, however, mature leaves were least efficient, followed by very young, young, and senescent leaves. Maximum transpiration rates for leaves of various ages did not vary much, however, except for a very low rate in senescent leaves. Few shrub species have been studied in such detail as *Rhagodia baccata* as to gas exchange characteristics of leaves of various ages.

Cunningham and Strain (1969) found that the amount of water available to the California shrub *Encelia farinosa* determined not only the quantity of leaves but also the leaf structure. Under water stress the plant produced smaller leaves with very compact mesophyll tissues and greatly reduced intercellular spaces. These small dense leaves showed lower rates of net photosynthesis and transpiration.

It might be assumed that the photosynthetic and transpiration responses of shrubs at a particular season of the year could be strictly a function of the proportion of leaves in various age classes. However, acclimation--changes in the gas exchange response to certain sets of environmental factors-- can take place over a much shorter period of time. The studies mentioned earlier by Strain and Chase (1966) demonstrated acclimation to take place after plants had been in the growth chamber for only 7 to 17 days. It is unlikely that the proportion of leaves in various age classes changed appreciably during this period of time. Net photosynthesis and transpiration response to temperature were found to change after a 24-hour pretreatment at high or low temperatures in *Encelia californica* (Mooney and Shropshire 1967; Mooney and Harrison 1970). A pretreatment at 30° C. was particularly effective.

Seasonal or short-term acclimation of shrub gas exchange, whether caused by changes in leaf age, structure, or physiology, is an added challenge to efforts to construct quantitative models of net photosynthesis or transpiration as a function of environmental parameters.

Diel patterns of gas exchange

Diel patterns of net photosynthesis and transpiration can assume sundry forms. Hellmuth (1971) found that western Australian shrubs under optimal moisture conditions always showed a single daily peak of activity for both net photosynthesis and transpiration. These gas exchange rates corresponded with maximum irradiation and optimal leaf temperature conditions. Under moisture stress, only a few species maintained this single-peak pattern. Other species showed bimodal or multipeak daily patterns of net photosynthesis and transpiration. Because the patterns of net photosynthesis and transpiration for a given species at a particular time of year are usually parallel, changes in stomatal aperture are often suspected as the causative agent of the two-peak or multipeak pattern (Lange and others 1969).

High leaf temperatures might exceed optimal values for the carboxylation reactions of photosynthesis and thereby cause a midday depression in photosynthetic rates independent of any stomatal movement. Raschke (1970) has recently shown that even though stomatal conductance at temperatures between 15° and 35° C. is roughly proportional to net photosynthesis, at higher temperatures stomata may be fully open while net photosynthesis declines and finally becomes negative. Nevertheless, because transpiration is usually closely correlated with net photosynthetic activity, stomatal closure is usually implicated in these midday depressions. Closure imposed by plant water stress or high leaf temperatures or a combination of both may be responsible for the reduced stomatal conductance at midday (Hellmuth 1971; Lange and others 1969). Relative humidity may also play a role here (Lange and others 1969; Tranquillini 1963).

Partitioning resistances to gas exchange

The control mechanisms of plant gas exchange have received considerable study in recent years. Although stomatal control has long been recognized, only during the last 20 years has there been a substantial effort to quantify its importance in respect to other limiting factors of plant photosynthesis and transpiration.

Gaastra's Formulation

Gaastra (1959) was the first to present and employ a clear formulation of the relation of stomatal diffusion resistances for water loss and CO_2 uptake by leaves to other resistances. A model is presented in figure 1; the equations for transpiration and photosynthesis are

$$Tr = \frac{[H_2O]_a - [H_2O]_{int}}{r_a + r_s} \qquad (1)$$

$$Ps = \frac{[CO_2]_a - [CO_2]_{chl}}{r'_a + r'_s + r'_m} \qquad (2)$$

By an equation analogous to Ohm's law, photosynthesis and transpiration are represented as fluxes responding directly to the concentration gradient of these gases and indirectly related to the magnitude of the resistances to diffusion. For transpiration, Tr, the driving gradient is simply a concentration difference in water vapor between the evaporating surfaces of the leaf interior, $[H_2O]_{int}$, and the ambient atmosphere $[H_2O]_a$. For CO_2 uptake by the leaf, the driving force is the diffusion gradient between the ambient atmosphere, $[CO_2]_a$, and the site of CO_2 utilization in the chloroplast, $[CO_2]_{chl}$. In each process the resistances to diffusion are in series and can therefore be summed. Cuticular resistance, r_c, is of course in parallel with stomatal diffusion resistance, r_s (fig. 1), but as the magnitude of r_c is usually quite high compared to r_s, r_c is often ignored in the simplified models.

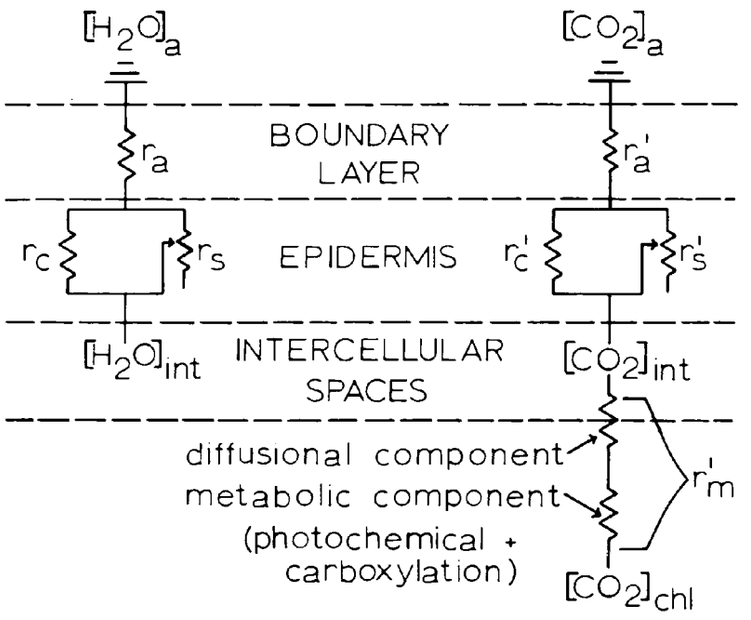

Figure 1.--Schematic representation of diffusional resistances to CO_2 and H_2O. The diffusion gradient for water vapor is between the ambient H_2O concentration, $[H_2O]_a$, and the concentration in the intercellular spaces, $[H_2O]_{int}$. The diffusion gradient for CO_2 is between the outside air, $[CO_2]_a$, and the concentration of CO_2 in the chloroplast following carboxylation, $[CO_2]_{chl}$. Diffusional resistances for H_2O and CO_2, respectively, are r_c and r'_c, cuticular resistance; r_a and r'_a, boundary layer resistance; r_s and r'_s, stomatal resistance; and r'_m, mesophyll resistance, made up of diffusional and metabolic components. Adapted from Gaastra (1959) and Monteith (1963).

The boundary layer and stomatal diffusion resistances for water vapor (r_a and r_s) and CO_2 (r'_a and r'_s) differ by a proportionality constant that takes into account the difference in diffusivity of these gases in air. Boundary layer resistance can be established from measurements of evaporation from leaf models or from convective heat coefficients determined for particular leaf forms. Once r_a is established, the r_s term is easily calculated from equation 1, on the assumption that the sites of evaporation from the mesophyll cell walls are saturated with respect to the prevailing leaf temperatures. Boundary layer and stomatal diffusion resistances, r'_a and r'_s, for CO_2 transport can now be easily calculated from r_a and r_s, using the proportionality constant. The r'_m term is then derived from equation 2, with the concentration of CO_2 at the site of utilization of the chloroplasts assumed to be zero.

Gaastra used this method of partitioning resistances for transpiration and photosynthesis in several crop species and demonstrated that the r'_m term was quantitatively quite significant. Naturally, r_s and r'_s could vary considerably from very low values to approaching infinity with changes in stomatal aperture. Because r'_m is relatively large, however, Ps is much less influenced than Tr by such changes in boundary layer or stomatal resistances. This conclusion has been borne out in subsequent experimental work (Caldwell 1970a, 1970b).

Limitation of the formulae

Although Gaastra's formulation has been widely used during the past decade, some limitations of its assumptions and logic have been pointed out. There is some evidence to suggest that the evaporative surfaces in the interior of the leaf are not saturated with respect to leaf temperature. Whiteman and Koller (1964) estimated that a saturation deficit in the leaf interior of up to 300 bars might exist for the desert halophytic shrub *Reaumuria hirtella*. More recently, Jarvis and Slatyer (1970) compared transpiration rates with the flux of nitrous oxide through a leaf and suggested that under conditions of high transpiration rates and plant dehydration a mesophyll saturation deficit could develop in cotton plants.

In deriving r'_m, the mesophyll resistance, from equation 2, to assume that the concentration of CO_2 at the sites of carboxylation in the chloroplast is zero would ignore the fact that there must be an appreciable concentration of CO_2 to act as a

substrate in the carboxylation reaction. If the assumption is, however, that the CO_2 concentration is zero after the CO_2 has in fact been chemically combined to form phosphoglyceric acid or oxaloacetate this is certainly quite sound. However, the r'_m term then becomes more than a mere diffusion resistance, and can be partitioned into several components. Monteith (1963) envisaged a series of three resistances, a purely diffusional resistance that CO_2 encounters between the intercellular spaces and the chloroplasts, followed in series by carboxylation and photochemical resistances which together would make up the chemical or metabolic component of r'_m (fig. 1).

Since net photosynthesis is usually the result of concomitant photosynthesis and photorespiration, the r'_m term not only must take into account the diffusional resistances to CO_2 through the mesophyll wall and the metabolic resistances to photosynthesis, but also the efficacy of concomitant photorespiration. In its correct interpretation, the r'_m term is a catchall for all limitations to net photosynthesis except those encountered in the diffusional boundary layer and stomatal resistances. It would not be surprising to find that r'_m is large in comparison to r'_s and r'_a, as reported by Gaastra (1959) for several crop species and by Mooney and Harrison (1970) for the desert shrub *Encelia californica*.

To separate experimentally the diffusional component from the other components of r'_m, CO_2 concentration at the chloroplast has been estimated by the CO_2 compensation point for net photosynthesis, Γ (Bierhuizen and Slatyer 1964; Holmgren and others 1965; Whiteman and Koller 1967). Presumably at Γ there is no net flux of CO_2 between the intercellular spaces and the external atmosphere, and similarly no net flux between the intercellular spaces and the site of utilization in the chloroplast because $[CO_2]_{chl} = [CO_2]_{int}$ $[CO_2]_a$. The CO_2 compensation point is estimated either by allowing the plant to remove CO_2 to an equilibrium value in a closed chamber system or by extrapolation of Ps as a function of $[CO_2]_{int}$ (Whiteman and Koller 1967; Samish and Koller 1968). Using Γ as $[CO_2]_{chl}$ in equation 2 should provide a calculation of the diffusional component of r'_m. Although something is gained by partitioning the diffusional component of r'_m from the metabolic components, this calculation is at best only a rough approximation. There is no assurance that $[CO_2]_{chl} = \Gamma$ under normal conditions when $[CO_2]_a$ = 300 p.p.m. Furthermore, since the resistances between the loci of respiratory CO_2 production and photosynthetic CO_2 uptake in the mesophyll tissue (fig. 2) are largely unknown quantities, there is no assurance that $[CO_2]_{chl}$ is equivalent to $[CO_2]_{int}$ at Γ. Not only will photorespiration influence Γ but it will also affect the estimation of the diffusional component of r'_m. This value will depend largely on the unknown diffusional resistances separating the sites of CO_2 production and utilization in the mesophyll tissue. Certainly for plants which apparently lack photorespiration it is easier to estimate the diffusional component of r'_m. For species that do possess photorespiration, the error in estimating the influence of photorespiration on r'_m can be minimized by conducting experiments at low ambient oxygen concentrations (Troughton 1969; Troughton and Slatyer 1969; and Lake and Slatyer 1970). They estimated total r'_m as

$$r'_m = \frac{d[CO_2]_{int}}{d\ Ps}$$

The internal leaf concentration of CO_2, $[CO_2]_{int}$, was determined by passing air of known CO_2 concentration through the leaf. By using nitrogen instead of air as the carrier gas they could determine the influence of photorespiration on r'_m. However, they still could not distinguish with certainty the magnitude of the diffusional and metabolic components of r'_m. Rackham (1966) took a completely different approach and estimated mesophyll diffusional resistances from liquid diffusion rates of CO_2 in conjunction with microscopic observations of mesophyll cell dimensions.

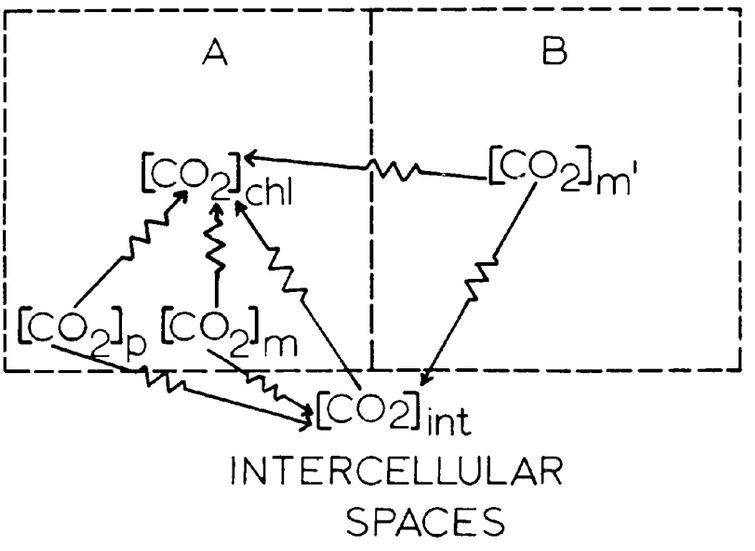

Figure 2.--Schematic representation of CO_2 fluxes and resistances within the mesophyll tissue. Two cells are represented: a photosynthesizing cell (A) and a nonphotosynthesizing cell (B) in the mesophyll tissue. Carbon dioxide is being produced in the peroxisomes, p, and in the mitochondria of the photosynthesizing cell, m, and of the nonphotosynthesizing cell, m'. Carbon dioxide is being taken up in the chloroplast, chl. Adapted from Jackson and Volk (1970).

Several investigators (Moreshet and others 1968; Gale and Poljakoff-Mayber 1968; and Koller 1970) also suggest that the component resistances for plant gas exchange may be incorrectly estimated by using the original formulation of Gaastra (1959). They point out that with anisolaterality of the epidermal surfaces and the underlying mesophyll tissues, and appreciable resistance to gaseous diffusion between the upper and lower layers of the mesophyll, true values for r'_s and r'_m deviate substantially from those estimated by the original formulation. Future studies of resistance partitioning for plant gas exchange should certainly take into account the model recently proposed by Koller (1970) (fig. 3).

Control of plant gas exchange

Despite the limitations and ambiguities associated with much of the work to date, past research is of great value in indicating the magnitude and the degree of control exerted by the different resistances to water vapor and CO_2 transport.

Whiteman and Koller (1967) investigated the diffusive resistances to CO_2 uptake in several desert shrubs of Israel. The magnitude of r'_s and r'_m varied considerably between species. In several species, changes in net photosynthetic rates were closely correlated with changes in r'_s. In other species, however, changes in net photosynthetic rates occurred with no change in r'_s values. Estimates of the diffusional components of r'_m varied between species by a factor of 10. Those shrubs having extremely low

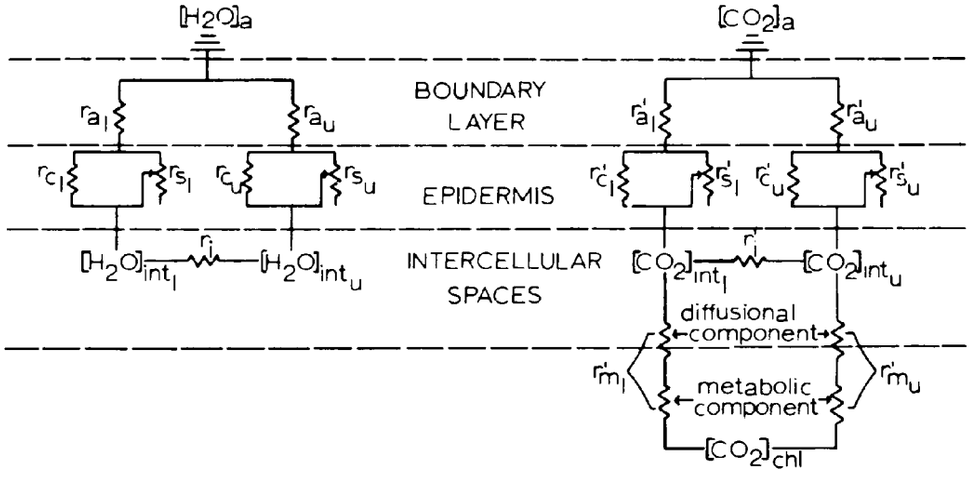

Figure 3.--Schematic gas diffusional model. Symbols are the same as for figure 1. In addition, u and l indicate resistances for the upper and lower sides of the leaf respectively; and r_i is an internal diffusional resistance between the upper and lower mesophyll tissue. Adapted from Koller (1970).

values (1.5 to 2.5 sec. $cm.^{-1}$) were characterized as particularly well adapted. Whiteman and Koller suggest that the most successful desert shrubs would be those which combine a very small r'_m with a large r_s and very responsive stomatal action so as to minimize water loss and maximize net daily CO_2 gain.

The importance of diffusional resistances has been implied by Cunningham and Strain (1969) in their investigations of leaf variability in the desert shrub *Encelia farinosa*. Leaves of this species formed during periods of moisture stress tend to be smaller than leaves formed during periods of ample moisture. They also have more pubescence and a more compact mesophyll with much less intercellular space. Gas exchange characteristics of these small compact leaves suggest that net photosynthesis and transpiration per unit dry weight of leaf material are much less than in leaves of the same plants formed during more optimal moisture conditions. Unfortunately, there was no attempt to partition the resistances to gas exchange in this study. Certainly, the r'_a component might be expected to increase with increased pubescence. Also, the more compact mesophyll tissue may well be responsible for a higher value of the diffusional component of r'_m, which would also be expected to reduce net CO_2 uptake. No information was given concerning stomatal response of these two types of leaves.

Wilson and Cooper (1970) selected for small mesophyll cell size within a population of *Lolium perenne* and found that such individuals did indeed have higher net assimilation rates. There was no partitioning of resistances, but selection for smaller mesophyll cells and presumably smaller values of r'_m apparently does result in greater photosynthetic rates and also greater crop yields.

The metabolic or chemical component of r'_m as influencing net photosynthetic rates has been studied. Examples of findings include alterations of the photochemical component of r'_m by impairment of photoreaction II when ecotypes of *Solidago virgaurea* from shaded habitats were grown in intense illumination (Bjorkman 1968). The carboxylation component of r'_m was also found to be inherently different in different ecotypes. Bjorkman found that carboxydismutase activities and photosynthetic rates were higher in ecotypes of *Solidago virgaurea* from exposed habitats than in ecotypes from shaded habitats. Inherent differences in carboxydismutase activities, if reflected in higher net photosynthetic rates, would certainly be expressed in differences in the chemical component of r'_m.

Hatch, Slack, and Bull (1969) found that several key enzymes associated with carbon fixation in corn and *Amaranthus* plants could be substantially altered in activity by exposure of the plants to high and low light intensities over long periods of time. They found that the content of glyceraldehyde 3-phosphate dehydrogenase, adenylate kinase, and pyrophosphatase were twice as high in plants grown in high light conditions as in those grown at low light. Pyruvate, Pi dikinase, and phosphopyruvate carboxylase were between 5 and 10 times more active in the high light intensity group. Plants in the low light group upon transfer to high light intensities for 6 days were found to have enzyme activities equivalent to those of plants grown continually at high light. Maximum net photosynthetic rates paralleled the increases in enzyme activities in this plant group. These results suggest that the chemical component of r'_m can indeed be substantially altered in the same plants with different environmental pretreatments.

Mooney and Harrison (1970) found that higher temperature pretreatments could alter total r'_m (diffusional plus metabolic components) by twofold in less than 24 hours. Although the components of r'_m were not partitioned in this study, it was found that the degree of oxygen inhibition of net photosynthesis in this shrub was also substantially altered within the 24-hour period. This would suggest that the chemical component of r'_m had been modified. Similarly, Caldwell and Camp (unpublished data) found that the degree of oxygen inhibition of net photosynthesis in *Atriplex confertifolia* could be substantially altered within 36 hours of exposure to elevated temperatures.

Troughton and Slatyer (1969) measured r'_m in oxygen-free air to minimize the influence of photorespiration. They found that neither leaf temperature nor water stress affected r'_m under these conditions in cotton leaves. However, Gale and Poljakoff-Mayber (1970) found that r'_m underwent a substantial change when *Atriplex halimus* was cultured under differing degrees of salinity.

Conclusions

Certainly partitioning of resistances for plant photosynthesis and transpiration is a useful tool in elucidating the inherent differences in gas exchange rates of various shrub species and the mechanisms of photosynthetic acclimation. The technique can be performed on intact plants, thus avoiding destruction of the structural integrity of the physiological systems. The exact meaning of the partitioned resistance components must be recognized, however. For example, r'_m as originally defined by Gaastra is extremely ambiguous and may often be overestimated if leaves are anisolateral or possess a significant internal diffusion resistance between the upper and lower portions of the mesophyll tissues. In the future, efforts should be made to minimize the influence of photorespiration on the estimate of r'_m and to employ the expanded model of Koller (1970) to yield quantitatively correct estimates of these resistances.

Analysis of gas exchange resistances also has practical value as an aid to systematic genetic selection for higher photosynthetic rates or more efficient water use by shrub species. For example, biotype selection for low r'_m and higher r_s values could be practiced in breeding programs to enhance the water use efficiency of photosynthesis in arid land shrubs.

The C_4 metabolic pathway

Since the relatively recent discovery of an alternate pathway of CO_2 fixation in species such as sugar cane and corn (Kortschak and others 1965; Hatch and others 1967) which have been traditionally acclaimed for high net photosynthetic rates and high crop productivity, there has been a flurry of research concerned with the metabolic and gas exchange characteristics of such species. Since the C_4 dicarboxylic pathway also appears in numerous shrub species primarily associated with warm and arid environments (Welkie and Caldwell 1970), the implications of this alternative photosynthetic pathway are quite germane to the present discussion.

Among the many physiological and anatomical characteristics consistently associated with the C_4 pathway (Hatch and Slack 1970) are those which imply that C_4 plants are particularly well adapted and productive in arid environments. In contrast to plants that fix carbon by the normal C_3 pathway, C_4 plants have low CO_2 compensation points for net photosynthesis, have little or no apparent photorespiration, have unusually high optimal temperatures for maximum net photosynthesis, require very high irradiation intensities for saturation of net photosynthesis, and generally have high net photosynthetic rates (Hatch and Slack 1970, Jackson and Volk 1970, Bjorkman 1970). In addition, net photosynthesis of C_4 plants is not inhibited by oxygen as it is for C_3 plants (Bjorkman 1970). It would seem then that such plants are ideally suited for survival and high productivity in warm environments with high irradiation intensities.

Most of this comparative physiological research has been carried out on laboratory- or greenhouse-grown plant material and usually on agronomically important species. Some excellent comparative studies have also been performed on species pairs in the *Atriplex* genus where one species possesses the C_3 and the other species the C_4 pathway (Bjorkman 1969; Bjorkman and others 1970; Bjorkman and others 1971; Osmond 1969; Osmond and others 1969; Slatyer 1969, 1970). Bjorkman and others (1970) found that like corn and other C_4 monocotyledons, *Atriplex rosea* lacked photorespiration and also lacked an apparent inhibition of net photosynthesis by oxygen. The quantum requirement for *A. patula* (C_3) is less when measured at low oxygen tensions than for *A. rosea*. This suggests that the C_4 metabolism is not inherently more efficient, and may, in fact,

be less efficient than C_3 metabolism. Nevertheless, the apparent lack of photorespiration in C_4 plants results in higher net carbon gain under optimal conditions of high light intensity and reasonably high temperatures. At low light intensities and low temperatures, however, *A. rosea* showed no advantage in net photosynthesis. Growth analyses of these two species paralleled net photosynthetic responses. Under ample moisture conditions there was no apparent difference in the range of r_s values.

Comparative physiological studies of *A. spongiosa* (C_4) and *A. hastata* (C_3) (Osmond and others 1969; Slatyer 1969, 1970) revealed, for the most part, a parallel story to the comparative studies by Bjorkman and others (1970). However, *A. spongiosa* was found to have a consistently higher r_s than *A. hastata*, even though the stomates of *A. hastata* were somewhat more responsive at severe water stress. In addition, cuticular resistances for *A. spongiosa* were four times higher than for *A. hastata*. The ability to curtail water loss was, needless to say, much greater in *A. spongiosa*, particularly at limiting moisture conditions. In addition to the lack of photorespiration, *A. spongiosa* had lower r'_m values than *A. hastata* even when measured at low oxygen tensions to minimize photorespiration in the determination of r'_m (Slatyer 1969, 1970). With increasing water stress, r'_m was not found to vary in either species. Slatyer (1970) found that *A. spongiosa* had consistently lower transpiration rates and greater water use efficiency than *A. hastata* for both single leaves and whole seedlings. This was attributed to the lack of photorespiration, the lower r'_m and the higher r_s and r_c values found in this species.

Such comparative studies, based primarily on gas exchange characteristics of single leaves, do not, however, describe the performance of the whole plant in field conditions. Crop plants possessing the C_4 pathway such as corn and sugar cane are traditionally known for very high productivity; however, this may not be the case for wildland plants. Slatyer (1970) analyzed growth of *Atriplex spongiosa* and *A. hastata* over a 23-day period. Net photosynthetic rates per unit leaf area of *A. spongiosa* were indeed usually higher and never less than those of *A. hastata*. However, although total leaf area was initially greater in *A. spongiosa*, toward the end of the experiment total leaf area per plant became much less than in *A. hastata*. Therefore, the daily growth rate of *A. spongiosa* actually fell below that of *A. hastata* in the latter part of the experiment. Young greenhouse-grown plants were used in these studies, and it is difficult to extrapolate these results to field conditions with higher degrees of mutual leaf shading, imposed moisture stress, and seasonal variability in gas exchange rates.

Jones and others (1969) estimated maximum growth rates of *Atriplex nummularia*, a C_4 shrub, to be in the same range as sugar cane and corn, based on a 500-day growth analysis of plants in an open and immature community.

Studies currently underway to compare gas exchange rates throughout an entire season for two perennial shrub species, *Atriplex confertifolia* (C_4) and *Eurotia lanata* (C_3) (Welkie and Caldwell 1970) may help to evaluate relative advantages and disadvantages of the C_4 metabolic pathway in the field (White, Moore, and Caldwell, unpublished data). Although not in the same genus, these species are in the same family and grow in the same ecological niches. Three-year standing crop estimates from monospecific communities of *Atriplex confertifolia* and *Eurotia lanata* suggest that total shoot plus below-ground standing crops are nearly the same in these two communities even though annual shoot productivity is somewhat higher for *Atriplex* (Bjerregaard and Caldwell, unpublished data).

If C_4 shrub species are indeed highly superior in productivity and adaptability to arid lands in the final analysis, a great deal of effort might be centered on the use of such shrub species. Attempts to breed the C_4 metabolism may be worth pursuing; however, initial indications are rather discouraging. *Atriplex patula* X *Atriplex rosea* F_1 and F_2 hybrids, although intermediate in many anatomical respects, have proven to be definitely inferior to both the C_4 and C_3 parents in terms of CO_2 uptake (Bjorkman and others 1971).

Carbohydrate reserves and response to use

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Because horticulturists, foresters, rangeland managers, and certain kinds of biologists share an interest in growth, production, and physiological well-being of woody plants, they also share prime technical concern about seasonal trends in accumulation and depletion of the so-called food reserves or certain carbohydrates in woody plants. These basic organic substances are the *available* or *nonstructural* carbohydrates such as sugars, fructosans, dextrins, and starch which are mobilizable and available within the plant for its nutrition and development. The importance of mobilizable or nonstructural carbohydrate is, of course, due to strong interrelationships with plant growth, reproduction, respiration, and the synthesis of all other organic compounds found in plants.

Woody plant literature

There have been many investigations of seasonal trends in carbohydrate accumulation, utilization, and response to environment and the cultural practices for various crop plants. To date, much of the investigation of woody plants has involved work on fruit and forest trees, and these sources are apparent in summaries of tree physiology by Kramer and Kozlowski (1960) and Kozlowski and Keller (1966). Likewise, the findings of horticultural and forest physiologists are also prominent in the review by Priestly (1962) on carbohydrate resources within perennial plants. As Priestly pointed out, the general pattern of carbohydrate accumulation in fruit trees was known in the late 1800's. However, in this century, man has added voluminous pieces of specific knowledge about individual carbohydrates, quantities involved, and related matters of biochemistry and physiological function.

We have learned from various works including Kraybill and others (1930) that, of the carbohydrates mentioned previously, starch is the most abundant one in apple trees; whereas, from literature on forage plants, we know sucrose and fructosans are usually the major storage materials of grasses. But dextrans and starch are found in some grasses, and Garrison (1966) reported starch in a sedge. Numerous workers, among them Beattie (1948), Smyth (1934), and Karmarkar (1934), have provided quantifications of seasonal trends in levels of carbohydrates in apple twigs. Inherent in the trends and timing reported are all the implications that respiration, new twig and leaf production, plus fruit production, reduce the reserves, whereas with renewed photosynthetic activity and reduction of annual growth and production, the carbohydrate reserves are replenished. There is also much direct evidence to support the correlative relationships of cyclic

phenological stages with levels of carbohydrate accumulations. It should be acknowledged though that also involved are complexities of factors such as rate of conversion of carbohydrate to new tissue, hormonal activity, various environmental effects, and man's cultural or manipulative practices, e.g., fertilizers, growth regulator sprays, and pruning.

With our present focus on matters that are especially germane to shrub utilization, it is of interest that Wenger (1953) studied the effect of severe cutting on sweet gum (*Liquidambar* sp.) and showed that the depletion of carbohydrates in the trunk was proportional to the total new growth of shoots. Kramer and Kozlowski (1960) and Kozlowski and Keller (1966) state that shoot growth largely depends on food synthesized the preceding year and that secondary or diameter growth in some woody species is dependent upon current photosynthesis for its supply of carbohydrates. As for an interrelationship of vegetative and reproductive partitioning of the carbohydrates, the literature is replete with testimonies about flowerbud formation in fruit trees being delayed or reduced if there has been excessive stimulation of vegetative growth. The stimulation can be the result of pronounced heading-in type of pruning, heavy application of irrigation, or of some fertilizer programs. Consideration of carbohydrate supply changes in relation to twig production and fruit production leads us to works on distribution of carbohydrates among various plant parts, and especially about possible degree of loss in reserves through pruning. Murneek (1942) showed that young apple wood (1 to 3 years old) had a higher concentration of carbohydrates than various other parts of the aboveground structure; however, actual total amount of carbohydrate present was greatest in old wood because it forms the major part of a plant's top. Kramer and Kozlowski (1960) also state that tops of forest trees are the primary carbohydrate reservoir. But is this likewise a verity for all true shrubs?

Shrub studies

Techniques

We are fortunate to have a considerable fund of information about physiology of trees and techniques of study, but there are still limitations in its application to shrubs. Investigations of trees have huge labor and technique problems in excavating and sampling the whole mature tree. And those investigators who have tackled the task were forced to accept little or no replication. As a consequence, work with whole mature trees or even whole tops is uncommon. Many studies of carbohydrate resources of trees are restricted to a composite sample of twigs of a certain age from a few trees. Kraybill and others (1927) set good guidelines of reliability when they suggested that 12 trees be sampled individually for each observation period. In work with shrubs such as performed by McConnell and Garrison (1966), replication was considerably less trouble than in work with trees, and for them whole shrubs and various parts of shrubs constituted a sample for physical measurement and chemical analysis of both percent and total carbohydrate. Yet as these workers can attest, when the chosen shrub *Purshia tridentata* requires that for complete recovery the root excavations go down to a depth of 7 to 12 feet (about 2.1 to 3.7 m.), one is willing to settle for three entire root systems per observation. Whereas inclusion of tops of nine entire shrubs per treatment was quite feasible, and standard errors for analytical results on various subdivisions of the shrub top material were held to an average of 5.5 percent of the mean. The use of only three or four shrubs for observing carbohydrate resources or compositing subsamples for laboratory analyses has been the practice of some workers and may seem like an overly frugal procedure for fieldwork with shrub tops. Yet naturally, the number of species studied, number of treatments, number of years, and costs involved in chemical analyses sometimes do force closely restricted sampling upon shrub investigators.

Various procedures for laboratory analysis of available nonstructural carbohydrates have been used. However, it should be remembered that woody materials contain considerable starch and this greatly influences choice of laboratory methods. Priestly (1962)

argues for the dilute acid method of hydrolysis because of claimed high reproducibility of results. Smith (1969) makes a case for diastatic enzyme digestion, claiming that the technique using 0.2*N* H2S04 can destroy fructose, hydrolyze some unwanted structural carbohydrate, and fail to hydrolyze over 60 percent of some forms of starch. Each shrub investigator should review the nature of his potential samples and the literature on techniques before choosing an analytical procedure.

Physiology

Difference in the phenological timetable among woody plants is a pertinent reason for continued study of seasonal trends in carbohydrate levels of shrubs. Under a given set of site conditions, many woody species may initiate growth within a week or so of each other, but the timing of the remainder of their development can be quite diverse. In Texas, Halls and Alcaniz (1965) found at least three growth patterns for browse plants. In the far West, the shrub *Purshia tridentata* exemplifies an early flowering species, and the shrub *Chrysothamnus nauseosus* is rather late in flowering. Kramer and Kozlowski (1960) indicate that fluctuations in reserves are greater in deciduous species than in evergreens. Thus, different genera in their cyclic levels of carbohydrate accumulation are likely to "inscribe" their own curve or "signature" with considerable individuality as the season progresses. And in the management of rangeland shrub resources, the seasonal trends in carbohydrate reserves of key forage species are of considerable importance.

Purshia tridentata may be the first rangeland shrub in the United States to have been investigated as to its carbohydrate trends and resources in work done by McConnell and Garrison (1966). Results of laboratory analyses of *Purshia* showed well-defined seasonal changes in percent of concentration, as well as of actual weight, of nonstructural carbohydrates for all root and crown portions of *Purshia* (fig. 1). The changes in percent carbohydrate were well coordinated among plant parts with the exception of about a 3-week timelag for the small-diameter roots. Hence, all zones of carbohydrate reserves were apparently drawn upon in the course of annual growth. And of considerable importance in understanding the ability of *Purshia* to withstand or not withstand twig removal were additional findings that:

1. Nonstructural carbohydrates were at their lowest ebb in late June and early July and at their peak in mid-November.

2. Root material showed greater seasonal change in carbohydrate resources than top material.

3. Actual weight of nonstructural carbohydrate was greatest in the roots and next greatest in the top material over 1 year old. This is the reverse of findings for trees.

4. The smaller roots, those under 1/4-inch (about 6-mm.) diameter, had higher percent of concentration of carbohydrate and greater total weight of carbohydrate than larger roots.

5. Highest carbohydrate concentration attained by small roots was 16 percent.

These relationships were determined on plants which had been subjected previously to light or moderate use, and some of the findings were acknowledged to be possibly modified by clipping or browsing treatments, or by the year-to-year variation in shrub productivity described by Garrison (1953a).

Donart (1969) included two shrubs, *Symphoricarpos vaccinioides* and *Chrysothamnus viscidiflorus*, in his study of carbohydrate concentrations in some mountain range plants. He analyzed root material under 1/4-inch (about 6-mm.) diameter recovered from duplicate 1-foot cubes of soil per observation period. He determined that these two shrubs had

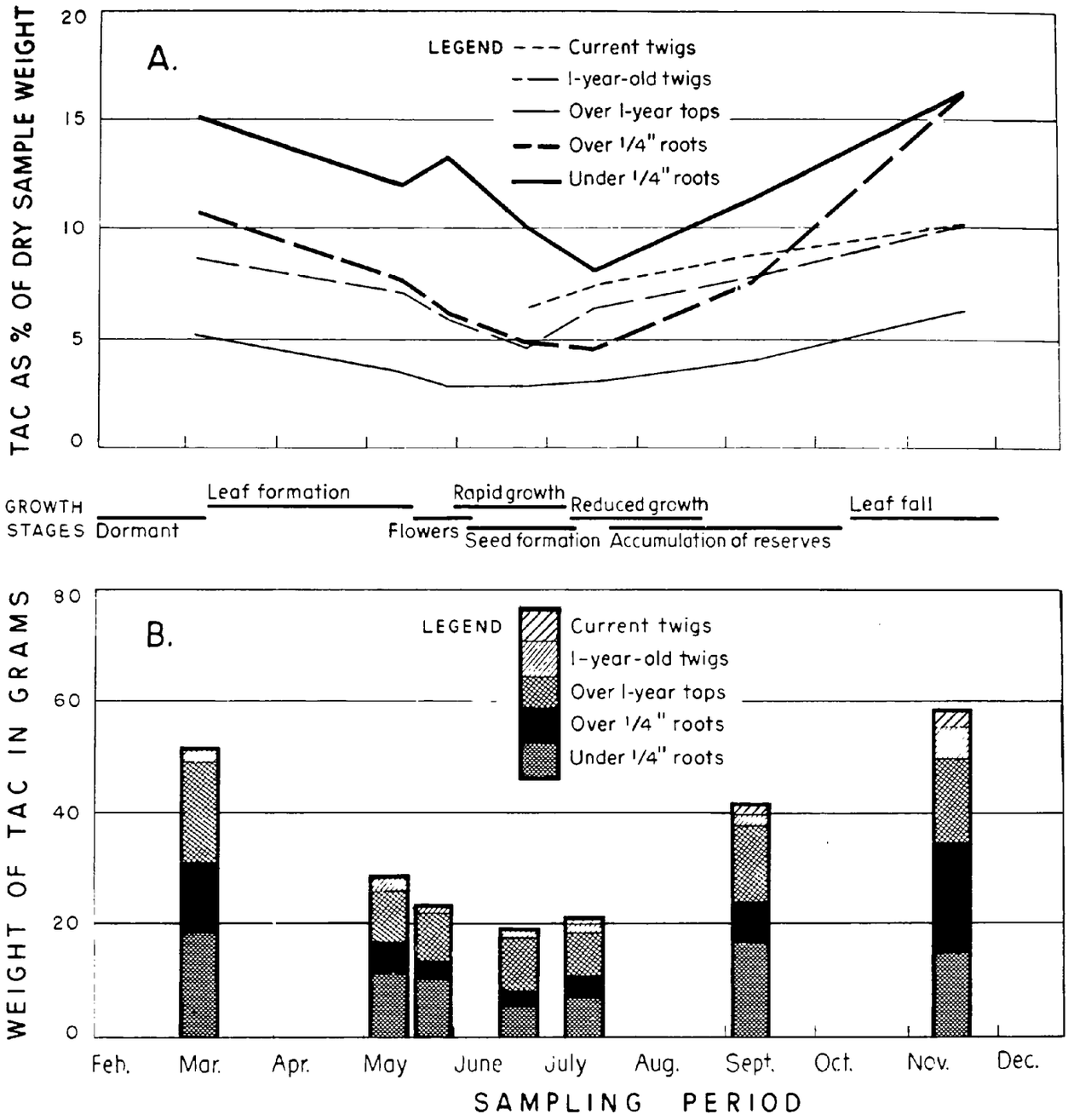

Figure 1.--Seasonal variation of total available carbohydrates in different parts of bitterbrush at seven phenological stages: A, *percentage of air-dry sample weight in nine tops and three root systems;* B, *total weight accumulations in three tops and three root systems.*

(1) a carbohydrate accumulation cycle consisting of depletion of root reserves with the onset of spring growth and recovery toward autumn, and (2) an unexplained fluctuation in carbohydrate concentration throughout the period of buildup in root reserves. In additional work by Donart and Cook (1970) on the same shrub species, a 90-percent clipping treatment was carried out at the time of low carbohydrate concentrations and at the period of maximum carbohydrate reaccumulation. (Carbohydrate maximums were about 16 percent for *Chrysothamnus viscidiflorus* and about 11 percent for *Symphoricarpos vaccinioides*.) It was learned that these two shrubs could restore their lost reserves by the time they had produced 20 percent of their anticipated regrowth.

Coyne and Cook (1970), working with three grasses and five shrubs (*Artemisia tridentata*, *A. arbuscula* var. *nova*, *Atriplex confertifolia*, *Atriplex nuttallii*,[1] and *Eurotia lanata*), also studied seasonal carbohydrate levels. The work included excavation of shrub roots to the 30-cm. level and sampling of roots which were 8 mm. or less in diameter. Crowns of shrubs were also sampled. The major findings for shrubs were:

1. Carbohydrate concentrations were consistently higher in the roots than in the crowns.

2. All shrubs except *Artemisia* showed the expected reduction in concentration of available carbohydrates in spring and the replenishment during late stages of phenological development.

3. With the exception of *Artemisia tridentata*, crowns and roots of shrubs showed similar trends in carbohydrate reserves although magnitude of storage and degree of fluctuation varied between parts of plants.

4. Low period of root reserves was in late winter for *Artemisia*, late April for *Atriplex confertifolia*, and early May for *A. nuttallii*.

5. A period of regrowth in fall can cause some reduction of carbohydrate reserves.

6. Highest concentration of available carbohydrate in the shrubs studied was about 17 percent for root material from *Atriplex nuttallii*.

Trlica and Cook (n.d.), working with the same shrub species as Coyne and Cook (1970), did further studies of concentration of carbohydrates using the same root and crown sampling procedures. Treatments, however, were applied which consisted of clipping of 90 percent of shrub crown at four dates during each of 2 or 3 years, and available carbohydrates were determined for root and crown samples after defoliated plants had regrown about 20 percent of mature size. Some of the most interesting findings were:

1. Most species defoliated by clipping about May 10 or July 1 had significantly smaller food reserves than did control plants by the fall season. Defoliations made about April 1 had less impact on food reserves.

2. *Atriplex nuttallii* had large food reserves and usually had greater regrowth after defoliation treatment than did other shrubs.

3. There was a direct relationship between average available carbohydrate levels in the autumn and the amount of regrowth made after defoliation treatment.

Production response to use

Response of growth or production of shrubs to utilization of twigs is, of course, a naturally related facet of this particular overview of shrub studies. Shrub production or clipping studies, as well as root excavations, may include a test of endurance for they can easily demand three to nine "backbreaking" field seasons from the investigator. Effects of clipping of twigs, or twigs and foliage, from shrubs have been studied in the United States by such workers as Julander (1937), Young and Payne (1948), Aldous (1952), Garrison (1953b), Lay (1965), and Cook and Stoddart (1963). It can be loosely generalized that many browse species can be safely utilized at about 50-percent removal of current growth of twigs during fall to late winter. Furthermore, removal of terminal buds or twigs generally stimulates twig production. This phenomenon has the common

[1]This is sometimes known as *Atriplex falcata* in Utah and Nevada.

physiological explanation involving apical dominance; i.e., when a terminal bud is damaged or removed, the lateral dormant buds are released for a time from the suppressing hormonal mechanism and two or more twigs develop as new leaders. This vegetative growth is often to the detriment of flower and fruit production.

Of course, some shrub species are not most productive of twigs at the 50-percent level of harvesting, and some behave as if they would only tolerate very light browsing. Removal of 75 percent of current twigs commonly appears to be too severe for prolonged utilization of most shrubs. However, attempts in Eastern United States to manage tree coppice stands for browse within reach of deer appear to warrant severe utilization in fall and winter. Because studies of response of shrubs to pruning are now numerous and diverse enough, an attempt at a tabular compilation of findings in the United States to date (table 1) seems to be in order.

Table 1.--*Compilation of pertinent items from some clipping studies on rangeland shrubs*

Geographic area	Species	Suggested level of use	Treatment levels studied	Length of study	Investigator
				Years	
Northern Arizona	*Populus tremuloides*	65 percent or less in summer	Four levels of controlled browsing and some clipping	3	Julander (1937)
	Cowania stansburiana	70-75 percent in winter	Utilization of plots and tagged twigs	3	
Northern Idaho	*Ceanothus sanguineus*	50 percent in the fall	50 percent, 75 percent, 100 percent at three periods	7	Young and Payne (1948)
	Amelanchier alnifolia	60 percent in the fall	do.		
	Lonicera utahensis	60 percent in the fall	do.		
	Rosa jonesii	60 percent in the fall	do.		
Lake States	*Thuja occidentalis*	Under 7 feet tall: less than 15-20 percent	0 percent, 25 percent, 50 percent in winter	7	Aldous (1952)
	Acer spicatum	Moderate to heavy[1]	0 percent, tips, 50 percent, 100 percent in winter	6	
	Betula alba var. *papyrifera*	Moderate to heavy	do.	6	
	Sorbus americanus	Light to moderate	do.	7	
	Cornus stolonifera	Light to moderate	0 percent, tips, 100 percent	5	
	Prunus pennsylvanica	Moderate to heavy	0 percent and 100 percent	5	
	Sambucus racemosa	Moderate	100 percent	5	
	Salix spp.	Moderate to heavy	0 percent, 50 percent, 100 percent	5	
	Fraxinus nigra	Moderate to heavy	tips and 100 percent	5	
	Corylus cornuta var. *cornuta*	Moderate	0 percent, tips, 100 percent	6	

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Table 1.--(con.)

Geographic area	Species	Suggested level of use	Treatment levels studied	Length of study	Investigator
Eastern Oregon and Eastern Washington	*Purshia tridentata*	60-65 percent	0 percent, 25 percent, 50 percent, 75 percent, and 100 percent in fall and winter	5 to 7	Garrison (1953b)
	Ceanothus velutinus	40 percent	do.	4 to 7	
	Chrysothamnus nauseosus	50 percent	do.	5 to 7	
	Holodiscus discolor	50-60 percent	do.	4	
	Cercocarpus ledifolius	50-60 percent for plants under 60-inch height	100 percent in pruning zone	4	
Great Basin Desert	*Artemisia tridentata* *Artemisia nova* *Atriplex confertifolia* *Atriplex nuttallii* *Eurotia lanata*	For all species and both phases I and II: (a) 30 percent for spring use or winter and spring combination (b) 50 percent use in winter periods	Phase I: 25 percent, 50 percent, 75 percent at four dormant periods Phase II: 30 percent, 60 percent, 90 percent at four periods including winter and spring seasons	Phase I, 4 Phase II, 4	Cook and Stoddart (1963)
Southeast Texas	*Ilex vomitoria*	25 percent	25 percent, 50 percent, 100 percent in the fall	9	Lay (1965)
	Ilex opaca	50 percent	do.	9	
	Symplocos tinctoria	25 percent	do.	9	
	Magnolia grandiflora	25 percent	do.	9	
	Fraxinus americana	Less than 25 percent	do.	9	
	Sassifras albidum	Less than 25 percent	do.	9	
	Three of above species plus 12 others	Something less than the treatment applied	Clipped 100 percent current growth every 3 months	3	

[1]"Heavy," nearly complete fall or winter harvest of current growth thought needed according to Aldous (1952) to maintain certain shrubs and trees within reach of deer.

Conclusions

There are many possible conclusions and inferences in the results of the studies, but we will mention only a few. Certainly the carbohydrate and clipping studies are helpful in determining and understanding the proper season and intensity of shrub use for perpetuation of the browse resource. Fall and winter seasons are the least detrimental periods for utilization. Late spring and the middle of the growing season, when carbohydrate reserves are the lowest, are the most damaging periods of use. Intensity of use which different species can tolerate is quite variable and may be related to magnitude of reserves as well as morphology of each species.

A new and important conclusion brought to light by this review is that although trees store most of their carbohydrate above ground, the preponderance of carbohydrate storage in true shrubs seems to be in the rather small diameter portions of the roots and secondly in the old heavy materials of the tops. Browsing generally removes only the young portions of the crown and not the major carbohydrate storage areas of the shrub. This may in part account for the remarkable tolerance of many rangeland shrubs to foraging by big game and livestock.

There are also many questions still unanswered about carbohydrate reserves in shrubs. Some of them needing investigation are:

1. Which of the common forage shrubs have greater carbohydrate reserves in roots than in tops?

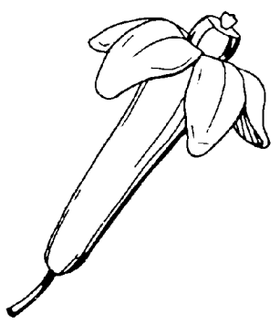
2. Can the critical periods and levels of carbohydrate reserves in shrubs be better defined than at present?

3. Are there moisture supply and temperature conditions at which carbohydrate reserves are most important and least important?

4. Are carbohydrate reserves closely related to degree of shrub productivity? If so, how can shrub reserves be increased?

5. What are the impacts of cultural practices (fertilizers, nutrient foliar sprays, growth regulator sprays, and a severe heading-in or pollarding treatment applied by domestic livestock or by machine) on carbohydrate accumulation patterns?

Many good studies have been carried out on carbohydrate resources and regimes in shrubs, yet there is much more work to be done.



Bud activation for regrowth

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Although the year-to-year survival of annual plants depends on their ability to produce seed, many perennial species survive adverse conditions by maintaining a reservoir of dormant meristems or buds. These meristems may grow either on the aboveground part of the plant--on twigs, branches, and trunks--or else below ground--on burls, crowns, stems, and roots. Because dormant buds can survive conditions which would damage actively growing shoot tips, the plant can begin new growth after cold or drought or regenerate after damage to the top growth.

Many aspects of the development and breaking of dormancy in plants have been reviewed recently by Alleweldt (1968); Champagnat (1965); Chouard (1960); Doorenbos (1953); Hemberg (1965), Romberger (1963), Samish (1954), Smith and Kefford (1964), Vegis (1964, 1965); Wareing (1956); and Wareing and Saunders (1971).

This chapter describes (1) the origin, development, and types of buds in woody plants; (2) the recognized types of dormancy and bud inhibition; (3) photoperiodism and dormancy; (4) correlative inhibition and apical dominance in herbaceous and woody plants; (5) seasonal growth patterns in shrubs; and (6) factors that affect regrowth in shrubs.

Origin and development of buds.--"A bud is an unextended, partly developed shoot having at its summit the apical meristem which produced it" (Romberger 1963). It is usually covered by primordial leaves and cataphylls (scales) initiated at some earlier time. Audus (1959) described buds as small islands of meristematic tissue left behind in mature tissue and protected by nonmeristematic bud scales.

Buds may be terminal, axillary, or adventitious. Terminal buds form at the tip of the shoot. Generally, in woody plants the terminal bud begins to form while the shoot is still actively elongating in the spring flush of growth. Buds form most often by the change of primordial development from foliar leaves to scales. The new bud may not be noticeable until near the end of the growth phase because it is hidden by the earlier formed but still expanding leaves (Romberger 1963).

After a prescribed number of primordia develop into scales, primordial morphogenesis changes to formation of foliage leaves (Foster 1932; Fulford 1966; Garrison 1949; Millington and Gunckel 1950). The foliage leaf primordia and their unextended internodes constitute the preformed shoot to be extended during the next growth flush.

Some plants, however, do not form morphologically distinct buds with scales. In *Hibiscus syriacus*, for instance, the embryonic leaves are protected by a ring of persistent floral peduncles (Tolbert 1961).

Little work has been reported on the seasonal morphogenetic cycle in buds of shrubs, but Schimper (1903) reported that many evergreen shrubs do not form true buds with bud scales. The terminal meristem is protected by developing leaves in an arrested state of development. Reeve (1942), however, found that in *Garrya* spp. (a sclerophyllous shrub genus in California) cataphylls are formed in early summer to late fall on lateral buds.

Axillary buds are initiated just above developing leaf primordia soon after the leaf is formed at the apical meristem. The axillary bud first appears as a mound of densely staining tissue sometimes above the second youngest leaf primordium (Sussex 1955). The pattern of subsequent development varies considerably, however. In some plants, the axillary meristem begins to form appendages immediately, as in many herbaceous species, but in others remains as a mound of tissue for some time and initiates its own leaf primordia later (Garrison 1949; Gifford 1951). In woody plants, the primordia, which may not be initiated for a year or more after the meristematic dome is determined, often develop into cataphylls. Development of scales and subsequent foliage leaves frequently overlaps the elongation of the shoot on which the bud is formed.

If an axillary bud does not grow out and become a shoot, it retains its position outside the cambium during secondary growth. It may remain visible outside the bark (Church and Godman 1966) or it may become buried in the bark and be apparent only by anatomical examination of that part of the stem. Such buds are called suppressed buds (Kormanik and Brown 1969). As the stem increases in diameter, the scales of the original bud are displaced laterally along the increased circumference of the trunk. As each of these scales may have an axillary bud associated with it, a cluster of buds forms on the stem. These clusters form the primary source of buds for epicormic sprouts which may grow out many years later in response to a stimulus, such as thinning, defoliation, or fire. In addition, axillary buds near the base of the epicotyl of the seedling may proliferate, as in *Betula* (Stone and Cornwell 1968) or scrub oak, *Quercus* (Berg, unpublished observations). As this portion of the shoot becomes buried, the resulting crown or burl develops as an underground structure. Thus, in many woody plants there is a tremendous potential for regrowth if the plant is damaged or if it is killed to ground level.

Adventitious buds may arise on callus tissue, stems, hypocotyls, or roots--almost anywhere but in the axils of recently initiated leaves. When adventitious buds develop on wound callus, they may arise from the phellogen (cork cambium) (Romberger 1963) or from internal meristemoids (Torrey 1966). Adventitious shoot meristems may arise from the pericycle or cortex in young roots (Bonnett and Torrey 1966), or from the vascular cambium or cork cambium in older roots (Brown and Kormanik 1967; Kormanik and Brown 1967; Priestley and Swingle 1929). Romberger (1963) states that adventitious buds rarely develop on stems except in relation to wound callus or clusters of suppressed buds. It is, however, difficult to prove the formation of adventitious buds in association with suppressed buds without careful analysis of serial anatomical sections.

Both suppressed buds and adventitious buds may play a role in resprouting of shrubs and trees. Woods and Cassady (1961) showed that the initial sprouting in two oak species (*Quercus* spp.) was from dormant buds. After these initial sprouts were removed, resprouting occurred from both dormant and adventitious buds. The latter developed from callus tissue which grew over the injured wood. Likewise after top removal, bitterbrush (*Purshia tridentata*) was observed to sprout from existing dormant buds and from adventitious buds formed on wound callus (Blaisdell and Mueggler 1956).

Dormancy.--Doorenbos (1953) used the term "dormancy" to apply to "any case in which a tissue predisposed to elongate does not do so." This usage is followed by Wareing (1956), Romberger (1963), and others. The simplest type of dormancy is inactivity imposed directly by cold, drought, or other unfavorable environmental conditions. We call this type of dormancy "quiescence" after the usage of Samish (1954).

Dormancy which is not a result of immediately unfavorable environment can be traced to an internal physiological condition. If the site of the physiological condition lies outside the dormant organ (in this case, the bud) it is termed "correlative inhibition." If the physiological condition lies within the bud, it is termed "rest." The terminology we have used follows that of Samish (1954) and Romberger (1963). Romberger (1963, p. 74) has reviewed the literature on dormancy and has compiled a table showing equivalent or near equivalent terminology of various authors.

These categories of dormancy--quiescence, correlative inhibition, and rest--are used as convenient reference points and are not intended to be mutually exclusive. All three types of dormancy may exist in a single organ, in turn, and may overlap in time (Doorenbos 1953). In a study of *Ribes nigrum*, for instance, Tinklin and Schwabe (1970) found that early in the season, while the new shoot was elongating, removal of the shoot tip caused outgrowth of several lateral buds (correlative inhibition). When removal of the shoot tip was no longer effective, defoliation of the shoot released the buds. Later in the season, however, removal of leaves became less and less effective as a means of inducing bud break. The buds were then considered to be in a state of rest which required several hundred hours of cold to break. If after the internal "chilling requirement" had been met, the plant did not grow because of cold, it was considered to be quiescent. Thus, dormancy is not a single nor a simple phenomenon.

Dormancy does not necessarily mean the cessation of growth but rather cessation of visible elongation. However, there are several meristems in a bud that may be active other than the subapical meristem (Sachs 1965). The apical meristem may continue to initiate leaf primordia and axillary bud primordia until late summer (Fulford 1966); the leaf primordia may be differentiating into scales or leaves; and floral primordia may be developing (Alleweldt 1968). Also, considerable physiological activity may be going on in the bud. Changes in major constituents, weight, and respiration have been measured in buds of *Fagus* (Gäumann 1935), *Prunus* (Thom 1951); and *Acer* (Pollock 1953).

Dormancy must be viewed as a developmental process in much the same way as flowering. In dormancy development, a bud undergoes morphological and physiological changes with various developmental functions operating in turn; e.g., inhibition of internode elongation, primordia forming scale leaves then later foliar leaves, physiological changes leading into rest, and then breaking of rest. Dormancy is, therefore, more than just growth inhibition and must be viewed as such (Smith and Kefford 1964).

Photoperiodism and dormancy.--Photoperiodism is the response of an organism to the relative length of day and night. In woody plants, rooting of cuttings, shoot growth, needle growth, leaf and fruit coloration, leaf abscission, cambial activity, dormancy induction, and floral induction have been shown to be responsive to day length (Nitsch 1957; Wareing 1956). In general, woody species respond to long days and short nights by shoot elongation, leaf growth, and cambial activity, and to short days and long nights by reduced elongation, bud formation, dormancy induction, and leaf abscission. Some woody plants have, on the other hand, been shown to be unresponsive to photoperiodism (Romberger 1963; Wareing 1969). Photoperiodism in woody plant species has been reviewed by Downs (1962), Nitsch (1957), Romberger (1963); and Wareing (1949, 1956).

Photoperiod may not always control the induction of dormancy, even in those species shown to be responsive under experimental conditions. Photoperiod response may, for example, occur only within a certain temperature range (Downs and Borthwick 1956;

Moshkov 1935); or temperature may completely override photoperiod in rest induction as in *Acer saccharum* (Olmsted 1951) or *Acer rubrum* (Perry 1962).

This condition of "rest" (Samish 1954) or "winter dormancy" (Doorenbos 1953) can be broken only by extensive exposure to low temperatures (20°-50° F.) in many species. A few plants do not require a chilling period, but resume growth in response to increasing day length (Wareing 1953, 1954). Other species will respond to an increase in photoperiod, but do so more quickly if they have been chilled (Wareing 1956; Romberger 1963).

As in herbaceous plants, the leaves are the site of photoperiodic perception. In most plants that have been studied, the expanding or recently expanded leaves are most sensitive (Alleweldt 1968; Nitsch 1957). Unexpanded leaves in the bud are able to respond to photoperiod in some cases, however (Wareing 1953).

Chouard (1946) proposed a scheme for classifying photoperiodic responses of woody plants. Nitsch (1957) modified it slightly and classified the photoperiodic responses of about a hundred species in 35 genera that had been reported in the literature. This classification scheme is as follows:

I. Long days prevent the onset of dormancy

  1. Short days cause dormancy

    A. Long days cause continuous growth — A

    B. Long days cause periodic growth — B

  2. Short days do not cause dormancy — C

II. Long days do not prevent onset of dormancy — D

Plants of class A grow continuously under long days, but stop growing completely under short days. Species of class B stop growing under short days, but grow by intermittent flushes under long day conditions. Class C plants grow without regard to day length, and class D plants go into dormancy even under long photoperiods although long days may prolong the growth period (Nitsch 1957).

Although a number of woody plants have been examined for sensitivity to photoperiod, the majority of species have not been tested (Nitsch 1957; Wareing 1956). In particular, very little is known about the effect of photoperiod and temperature on wildland shrubs. We do not know whether winter inactivity is caused directly by low temperature or whether it is rest induced by photoperiod and temperature. We do not know whether summer inactivity is caused by adverse moisture conditions, or whether it is a state of rest. Summer rest has been shown in *Poa scabrella*, a grass (Laude 1953); in *Lunularia cruciata*, a liverwort (Schwabe and Nachmony-Bascomb 1963); and in several species of *Allium* (Vegis 1964). All of these plants come from climates with a hot arid summer as do most shrubs of interest to this symposium. Much work on the effect of day length, temperature, and moisture on the seasonal growth and morphogenetic cycle is needed, therefore, in shrubs.

Correlative inhibition.--Correlative phenomena in plants are those in which one organ affects another at a distance (Sinnott 1960). The correlative phenomenon that we are concerned with here is the effect of other organs on bud outgrowth. This effect is usually considered in terms of inhibition by the terminal apex (apical dominance) or by leaves, but roots may be important by providing cytokinins which act to promote bud growth (Carr and Reid 1968; Chang 1970).

Correlative inhibition of buds has been a subject of critical study for about 60 years. Most early investigators favored the view that competition for nutrients between the apical and lateral bud meristems is the cause of apical dominance, the terminal meristem having a competitive advantage. This concept of bud inhibition, which came to be known as the nutritive theory, in essence held that apical dominance was but one aspect of quantitative correlation (Phillips 1969).

Another idea suggested as early as 1904 (Errera 1904) was that a diffusible bud inhibitor prevented bud growth. Even Loeb (1918) and Dostal (1926) at times interpreted their work in terms of direct inhibition rather than strict nutrient competition. Clearest evidence for a diffusible substance came from the early work of Snow (1925). In one experiment, he steam-girdled a stem. The bud below the girdle grew out even though the shoot above continued to grow (Snow 1929).

Auxin was recognized as a chemically discrete substance in the classical studies of Went (1936) and was soon implicated in correlative phenomena. Thimann and Skoog (1933, 1934) applied agar blocks containing auxin to decapitated bean plants. They showed that exogenously applied auxin could replace the shoot tip and inhibit the lateral buds, and that the degree of apical dominance depended on the concentration of the supplied auxin. They also showed that the excised shoot tip produced diffusible auxin. The theory based on this work was that auxin, produced in the terminal bud, inhibited the lateral buds by preventing them from producing their own auxin. Thimann (1937) later proposed a more general theory of auxin regulation of plant growth. In this scheme, each organ had its own optimum dose response curve with inhibition occurring from supraoptimum concentrations. The optimum for lateral bud meristems was considered lower than that for the terminal bud, and auxin, which was transported basipetally from the apex, inhibited the lateral meristems.

When the theory of direct hormonal control of lateral buds was proposed, Went (1936) and van Overbeek (1938) tried to reconcile the nutritional studies of earlier workers with their results with auxin. They proposed that auxin acted by diverting nutrients to the region where auxin was in highest concentration, i.e., the terminal bud or the site of exogenous application. Gregory and Veale (1957) also gave auxin a role in bud inhibition but proposed that auxin prevents completion of vascularization to the lateral bud. In a series of nutritional studies, they showed that under low levels of nitrogen in flax (*Linum* sp.), apical dominance was strong, while under high levels all lateral buds grew. Their interpretation was that under low nitrogen levels the meristems had to compete for nutrients, while under high levels all buds grew because there was no need to compete. Other workers have supported this idea, but give auxin the more direct role of creating a sink for nutrients (Booth and others 1962; Davies and Wareing 1965; McIntyre 1968, 1969).

As other classes of growth regulators have been characterized and surveyed, they have each in turn been implicated in some way in correlative inhibition of buds. Gibberellic acid has been reported to both enhance (Scott and others 1967) and to overcome (Wickson and Thimann 1958) bud inhibition. In general, gibberellins have been shown to increase growth of shoots which are already growing and in turn aid the suppression of lateral buds (Pharis and others 1965; Ruddat and Pharis 1966). Kinetin has been implicated more directly in lateral bud growth. Cytokinins, apparently produced in the roots, have been reported to break lateral buds in isolated stem segments (Chang 1970; Wickson and Thimann 1958). Application of kinetin directly to the lateral bud of an intact plant has caused the bud to grow even when the shoot tip is still present (Sachs and Thimann 1967; Panigrahi and Audus 1966).

Growth "inhibitors" have also been implicated in lateral bud control. Snow (1937) suggested that a special correlative inhibitor was present in stem tissue and that the formation of this inhibitor is enhanced by auxin. More recently the existence of

endogenous inhibitors has been well established, and several workers have demonstrated that correlatively inhibited buds contain higher concentrations of inhibitors than released buds (Dörffling 1963, 1964; Libbert 1964). Dörffling (1964, 1966) has also shown that inhibitors extracted from *Pisum* and *Acer* shoots prevented bud outgrowth in decapitated seedlings of the same species. Although these growth inhibiting extracts from plant tissue contain many compounds, most of the activity has been found to reside in a single substance--abscisic acid (Addicott and Lyon 1969; Wareing and Saunders 1971). Dörffling (1967) has demonstrated that abscisic acid was indeed present in the extract from pea shoots.

Correlative inhibition in woody plants.--Most of the work on correlative inhibition has been and continues to be carried out on herbaceous plants, but some work has been done with woody plants. The result of this work indicates that the basic mechanisms are the same in the two types of plants (Phillips 1969). Brown and others (1967) have pointed out, however, that "apical dominance" as defined for herbaceous plants (Thimann and Skoog 1933, 1934) is applicable only to the current year's growth in woody plants. They showed that in upright (excurrent) trees the lateral buds of the new growth were not subject to strong apical dominance, while axillary buds were strongly inhibited on the current growth of decurrent or spreading trees. They introduced, rather, the concept of "apical control" to differentiate between the growth forms of excurrent and decurrent trees.

In many woody plants, also, there is an overriding seasonal episodic character to growth (Doorenbos 1953; Romberger 1963). Tinklin and Schwabe (1970) have shown the seasonal changes in control of lateral buds in *Ribes nigrum*. They showed that lateral buds on the current season's growth are controlled in turn by the apex, the leaves, internal rest, and by low temperature quiescence, and that these types of dormancy overlap. It had long been known that defoliation of a tree during the summer would cause a new flush of growth (Fulford 1966), but Tinklin and Schwabe (1970) showed that as the effect of defoliation became lessened in late summer, removal of the bud scales increased the percentage of bud break. Thus, the leaves appear to play a more dominant role in correlative inhibition of buds in woody plants than in herbaceous plants.

Auxin has been shown to replace the upper part of a decapitated woody shoot in preventing bud outgrowth in a similar manner to herbaceous plants (Bowersox and Ward 1968; Plumb 1970; Vogt and Cox 1970). Gibberellic acid will cause terminal bud break and increase apical dominance over lateral buds by increasing terminal growth (Ruddat and Pharis 1966). Little work has been done with cytokinin involvement in lateral bud control of woody plants, but cytokinin activity was shown in root exudates of *Vitis vinifera* (Skene and Kerridge 1967).

Seasonal growth in shrubs.--Like other perennial plants, shrubs undergo cyclic changes in many physiological functions, such as vegetative growth, flowering, and quiescence or rest, during the course of a year. The changes in processes in the plant are a response to seasonal environmental changes--changes in temperature, day length, and available moisture. If shrubs of interest respond to day length, then they should respond to increasing day length by putting on new growth and by flowering and to decreasing day length by preparing for winter. Probably, however, most shrubs respond to temperature and moisture more than they do to day length. In native California shrubs from a Mediterranean type climate, for instance, anthesis usually occurs from March to June (Munz 1959). The actual time that anthesis occurs, however, varies considerably on a given site from one year to the next.

In a study of year-to-year changes in sprouting potential of chamise (*Adenostoma fasciculatum*), Laude and others (1961) showed that appearance of new growth varied by as much as 2 months. When their day/night temperatures are plotted after the method of Kimball and Brooks (1959), growth is shown to begin within a narrow temperature range of 53° to 61° F. day temperature and 38° to 42° F. night temperature. Flowering

in chamise has also been shown to be primarily under temperature control (Setchell 1925; Pequegnat 1951). Pequegnat (1951) reported that flowering is delayed in any given year by 13 to 18 days for each 1,000-ft. rise in elevation in the Santa Ana Mountains of California. Temperature also affects the rate of twig elongation in chamise (Miller 1947), but the duration of growth depends on whether the shoots are first-year sprouts (240 days), shoots of hedged plants (120 days), or branches of old mature plants (90 days) (Bedell and Heady 1959).

The most thoroughly studied seasonal change in relation to sprouting and growth, however, has been that of storage carbohydrate. Carbohydrate changes have been studied in grasses and forbs (McCarty and Price 1942), perennial weeds (Arny 1932), trees (Ishibe 1935; Tew 1970; Wenger 1953; Woods and others 1959), and shrubs (Hyder and others 1962; Jones and Laude 1960; D. G. Smith 1965). These studies reveal a direct relationship between sprouting and regrowth potential on the one hand and root or crown carbohydrate content on the other. In some cases, sprouting was considered desirable (McCarty and Price 1942; Tew 1970); in other cases, undesirable (D. G. Smith 1965; Wenger 1953). New growth depletes stored carbohydrates, so that starch levels are lowest near the end of the stage of most rapid growth. In trees, stored food is depleted first near the new growth, with the depletion spreading to the trunk and roots. The pattern of starch buildup in trees is not so clear, however (Ishibe 1935).

Changes in carbohydrates in shoots, crowns, and roots of *Adenostoma* were analyzed in relation to growth by Jones and Laude (1960). The most consistent correlations were shown with root starch reserves. The most rapid depletion occurred during the most rapid period of shoot elongation. Similar results were obtained by other workers with rabbitbrush (*Chrysothamnus* sp.) (Hyder and others 1962; D. G. Smith 1965), several species of *Quercus* (Woods and others 1959), and aspen (*Populus tremuloides*) (Tew 1970). Near the end of the spring flush of growth, the root and crown carbohydrates are lowest and the plants are most susceptible to damage from phenoxy herbicides (D. G. Smith 1965). If the plant is cut or burned to ground level at this time, vigor of sprouting is lowest (Jones and Laude 1960; McCarty and Price 1942; Tew 1970; Woods and others 1959).

Factors affecting resprouting in shrubs and trees.--The distinction between trees and shrubs is arbitrary but is reflected, in part, in the extent of stem and basal sprouting. Inherent in the concept of sprouting is the implication that buds begin to grow and form shoots from other than terminal or axillary position of the previous year's growth; and inherent in the concept of resprouting or regrowth is the assumption that something has happened to the plant to cause the activation of these stem, basal, or underground buds.

The actual stimulus may be normal yearly dieback in perennial grasses and forbs, browsing or grazing by domestic or wild animals, thinning of the stand or pruning of the plants, fire drought or insect damage to the plant, or chemical treatment. Any factor which causes an appreciable damage to the aboveground portion of the tree or shrub will cause stem sprouting and, if an underground reservoir of buds exists, will cause crown or root sprouting.

Perhaps the only factor which will cause sprouting without apparent damage to the plant itself is light. In numerous eastern hardwoods, for example, thinning or clear-cutting will cause epicormic sprouting on the boles or trunks of the remaining trees (Blum 1963; Jemison and Schumacher 1948; H. C. Smith 1965; Ward 1966). H. C. Smith (1965) has shown that the exposure of the bole of the tree to light is important, for he found that there was a significantly greater number of sprouts on the side of the tree next to a clearing than on the opposite side of the trunk. Vogt and Cox (1970) also demonstrated that shading one side of the base of an oak stump reduces the number and vigor of sprouts on that side.

If the aboveground portion of a woody plant is damaged, the extent and vigor of sprouting probably depend on the species, the extent of top removal or damage, the age and vigor of the plant, and the environmental conditions at the time of injury and following it. Certainly, sprouting is influenced by the carbohydrate reserves in the undamaged portions of the plant. The mechanism for such bud activation is unknown, but it has been conjectured that reducing the top growth causes an inbalance of hormones because of the change in root/shoot ratio (Doorenbos 1953). While auxin is almost certainly not the only hormone involved in preventing bud activation in shoots and crowns, it will prevent bud activation on sections of oak sprouts (*Quercus* sp.) Bowersox and Ward 1968), on decapitated ivy plants (*Hedera helix*) (Plumb 1970), and on oak stumps (Vogt and Cox 1970). Also, it is common practice to treat wounds from tree pruning with asphalt paints or emulsions containing high concentrations of auxins to prevent sprouting.

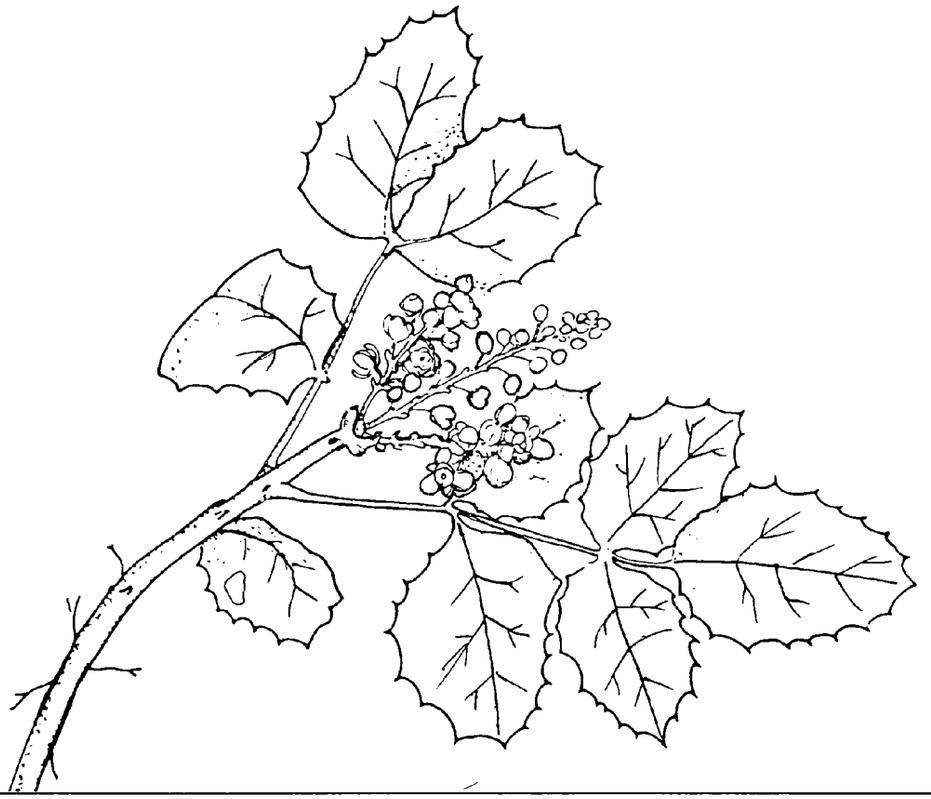
Resprouting after complete top kill or top removal by fire, chemicals, or mechanical means has been the subject of many investigations in forest, shrub, and shrub-grassland communities. These studies have had various objectives: increasing the vigor of regrowth to regenerate the forest stand (Wenger 1953), increasing vegetative propagation (Tew 1970), creating browse (Bedell and Heady 1959; Biswell and others 1952; Reynolds and Sampson 1943), preventing degeneration of valuable forage species (Blaisdell and Mueggler 1956), or reducing the vigor of regrowth or eliminating regrowth. Since the development of phenoxy herbicides, the killing of underground reservoir of buds has been studied by many investigators (Hyder and others 1962; Laude and others 1961; Perry and others 1967; Robertson and Cords 1957; D. G. Smith 1965; Upchurch and others 1969). Several of these studies have shown that the season in which cutting, burning, or chemical application is carried out is critical (Buttery and others 1959; Jones and Laude 1960) and that resprouting potential is most clearly related to carbohydrate reserves (D. G. Smith 1965). The timing of resprouting is probably affected by moisture availability and temperature (Laude and others 1961; Plumb 1961, 1963).

Resprouting after fire is of particular importance because fire can be an effective, inexpensive management tool if used carefully (Blaisdell 1953; Buttery and others 1959; Driscoll 1963; Ferguson 1957; Robertson and Cords 1957). Fire can be used to favorably change community composition by proper timing and frequency (Blaisdell 1953). If the timing is not correct, the stand can be changed to a less desirable composition. Change of community composition can be related to the relative sensitivities of various species to fire, i.e., in the differential ability to regenerate after burning. Species that have underground reservoirs of buds and carbohydrates can regenerate more rapidly than species which must start from seed (Blaisdell and Mueggler 1956).

Chemicals can be used to activate dormant buds as well as to control regrowth. For example, ethylene or compounds that release ethylene will, under some conditions, cause bud activation (Morgan and others 1969; Plumb 1970). Many of the chemicals listed by Crocker (1948) and by Doorenbos (1953) as causing bud break undoubtedly act through ethylene or ethylene-like compounds (Dollwet and Kumamoto 1970). Much work needs to be done yet, however, before ethylene-generating compounds can be used as effective tools in the field.

Section VI.

Nutritive Quality



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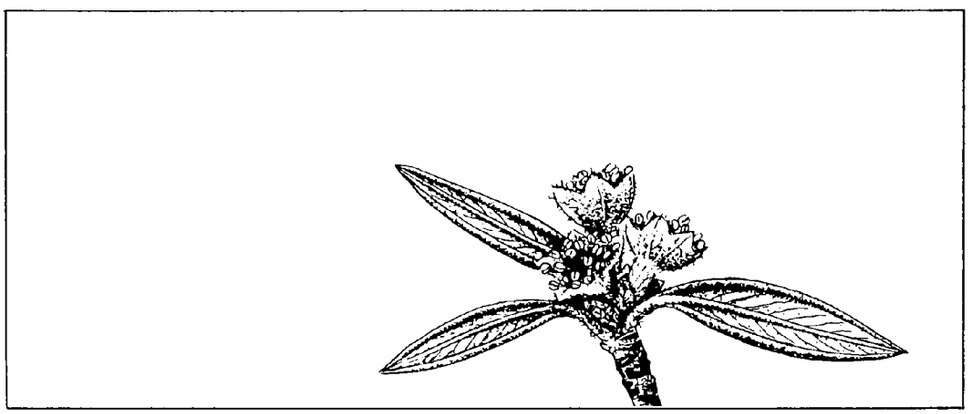

Nutritive value of shrubs

Donald R. Dietz

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"The primary driving force of all animals is the necessity of finding the right kind of food and enough of it. Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food supply."

These words by Elton in Van Dersal (1938) are even more true today where man's transgressions against land needed for livestock range and wildlife habitat are seriously threatening their continued existence.

To many animals, shrubs are food--sometimes their only food; thus the nutritional value of shrubs is of major importance to man and of *all importance* to the animals consuming them.

The nutritional value of shrubs has been studied from time to time by various researchers in the U.S.A. and in several other countries. A report by Chapline and Whyte (1947) entitled "The use and misuse of shrubs and trees as fodder" is quite pertinent to the subject and one of the important earlier contributions. They reported that shrubs provide forage for livestock throughout the Western United States when grass is not available due to drought or other conditions, and also when the nutritive values of grasses are below the minimum requirements for the maintenance of livestock. These authors stressed the importance of shrubs on the winter ranges of deer, bighorn sheep, and elk in the West.

The value of shrubs for winter feed on Utah's winter sheep range was pointed out by Esplin and others (1937).

Most of the nutritional investigations of wild plants, including shrubs, began in the United States in the late 1940's, although Knight and others (1911) reported on chemical composition of Wyoming forage plants as early as 1911 and Catlin (1925) published similar data for Arizona forages. Several major contributions toward knowledge of the nutritional value of range forage species include Gordon and Sampson (1939) reporting on composition of California Foothill plants; King and McClure (1944) presenting data on chemical composition of some American wild feedstuffs, and Savage and Heller (1947) discussing nutritional qualities of range forage plants in relation to grazing on the Southern Plains.

More recent studies of nutritional aspects of range forages including shrubs have been reported by Cook and Harris (1950) and Cook and others (1954). Smith (1957) reported on the nutritive value of some Utah browse plants in winter. A fairly complete review of nutritional aspects of range forage was presented by Sell and others (1959) during an intersociety forage evaluation symposium. At a more recent symposium, the present state of the knowledge in this field was discussed by Dietz (1970) and other authors. A report by Van Dyne and Kittams (1960) discussed interrelations among chemical constituents of forage samples including shrubs on foothill range in southwestern Montana.

Studies relating the nutritional value of shrubs to wild ruminants have been rather limited, but include reports of Swift (1948) and Silver and Colovos (1957) working with white-tailed deer in the northeastern United States. Ullrey and others (1964) studied digestibility of cedar *(Thuja occidentalis)* and aspen *(Populus grandidentata)* browse for white-tailed deer in Michigan. Short has also reported on digestibility studies with white-tailed deer in Michigan (Short 1963) and in Texas (Short, personal communication). Effects of cellulose levels on cell wall digestibility of shrubs by mule deer in Colorado was reported by Short (1966) and Short and Reagor (1970). Short and others (1966a) compared nutritional content of selected shrubs from different elevations and during seasonal growth periods in Colorado as did Dietz and others (1958, 1962b). Smith (1952, 1957) reported on nutritional values of shrubs in the Intermountain Region. Bissell and Weir (1957) and Bissell and others (1955) presented data on digestibilities of shrubs by deer in California. Studies on the nutritional value of shrubs have been conducted in the southwestern United States by Urness (1969), Reynolds (1967), Swank (1956), and others.

Important chemical constituents of shrubs

Because shrubs are important sources of food for both domestic and wild herbivores, there is a need to understand the mechanism involved in the production of important chemical constituents in shrubs and how these processes relate to animal requirements.

Protein

This nutrient is usually reported as crude protein. It is a measure of protein and nonprotein nitrogen multiplied by a correction factor, usually 6.25. For concentrates and feeds in general this factor is adequate, but 6.25 may be too high for roughages. The portion measured as crude protein may contain not only the various proteins such as simple proteins, conjugated proteins, and derived proteins, but also other nitrogenous compounds such as amides, amino acids, nitrogenous glucosides, ammonium salts, and others (Maynard and Loosli 1956).

Since our more valuable range animals are usually ruminants, both domestic and wild, true proteins are not so essential since protein is synthesized in the rumen from nitrogenous substances. Thus nitrogen and its various compounds are of more concern in ruminant nutrition than proteins and amino acids.

Protein is considered to be the most important nutrient component. A serious deficiency results in the failure of the body to maintain itself, while even a slight deficiency adversely affects reproduction, lactation, growth, and fattening processes. The ruminant animal needs protein for the rumen micro-organisms to digest and metabolize carbohydrates and fats effectively. If protein levels fall below a minimal level, rumen function becomes severely impaired.

Since crude protein content is significantly correlated to digestible protein content, determination of the crude protein level of a plant can give a reasonably reliable indication of its feed value (Sullivan 1962).

A brief summary of nitrogen relations between plants and soil is presented to aid in understanding the nitrogen content of shrubs. Nitrate in the soil is the most common source of nitrogen for plants; the reduction of nitrate to ammonia is a very important part of nitrogen metabolism. The energy for nitrogen metabolism results from the oxidation of carbohydrates, with ammonia combining with organic acids to form amino acids. Nitrates and nitrites are seldom found in the tops of trees under normal conditions (Kramer and Kozlowski 1960). Nitrates and nitrites are converted to ammonia by a reduction process in plant roots, thus nitrogen in leaves and stems is mostly in the form of ammonium compounds (Bonner and Galston 1952).

The amount of nitrogen compounds present in trees and shrubs varies with the kind of tissue, the age or stage of development, and the season. Nitrogen is associated with the physiologically active substances that occur in protoplasm and associated compounds such as enzymes, vitamins, nucleic acids, and others (Kramer and Kozlowski 1960). Leaves and meristematic tissues such as the cambium and tips of roots and stems contain most of the nitrogen concentration in trees and shrubs. Of the total nitrogen reported in apple trees by these two authors, 75 percent was in the roots and nearly 20 percent was in the leaves. In contrast, evergreen broadleaf orange trees had nearly 50 percent of the total nitrogen in the leaves, 10 percent in twigs, and 25 percent in roots (Cameron and Compton 1945).

While the leaves contain a large proportion of the total nitrogen, the phloem of the stem is also quite high in this element. Much of the nitrogen in the leaves of trees and shrubs is translocated to the stems during autumn before leaf fall occurs. As leaves mature, the proportion of cell wall material increases. This tends to modify apparent nitrogen content, and thus changes in nitrogen associated with plant aging are confounded with seasonal effects (Kramer and Kozlowski 1960). Nitrogen absorption by leaves of Gambel Oak (*Quercus gambelii*) and California black oak (*Q. kelloggii*) occurred very early in their development (Sampson and Samisch 1935). As the leaves matured, protein gradually decreased per unit of leaf area during the summer, followed by a rapid decrease in autumn. This was attributed by these authors to translocation of nitrogenous compounds out of the leaves. In autumn a considerable part of the nitrogen and minerals in leaves is translocated into the twigs before abscission occurs. This flow of nitrogen into leaves and then back into the stems coincides with physiological activity, and is quite important in the tree or shrub conserving nitrogen rather than losing it in leaf fall. In some species, however, a considerable part of the nitrogen (50-75 percent) has been lost during leaf fall (Murnech and Logan *in* Kramer and Kozlowski 1960). While little information is available concerning loss of nitrogen during leaf fall in wild shrubs, it might be an important factor in maintaining shrub vigor on ranges deficient in soil nitrogen.

Since ruminants can readily synthesize proteins from nitrogenous compounds, amino acid and protein relations in shrubs will not be discussed. In ruminant nutrition, we are concerned mainly with two factors: (1) Crude protein levels (N X 6.25 and (2) digestible protein (apparent digestibility of crude protein).

In general, shrubs contain higher percentages of crude protein during fall and winter than grasses and forbs, but lesser amounts during spring and summer. The leaves of shrubs contain higher percentages of crude protein than stems, and the tips of stems contain higher protein levels than the thicker mid and butt sections (Aldous 1945).

Differences in crude protein content of leaves and stems of some important shrubs found in the Black Hills of South Dakota are summarized in table 1. The decreasing levels of protein in both leaves and stems as the season progresses are evident. The stems of chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*) and western snowberry (*Symphoricarpos occidentalis*), however, showed an increase in protein from fall to winter. The comparatively high protein level in chokecherry winter stems

Table 1.--*Seasonal crude protein content in some important shrubs in the Black Hills of South Dakota. Ovendry basis.*

Species	Spring		Summer		Fall		Winter
	Leaves	Stems	Leaves	Stems	Leaves	Stems	Stems
	Percent						
Aspen	17.9	14.8	12.0	5.9	4.8	7.0	6.5
Chokecherry	21.9	17.4	15.2	9.5	6.6	8.8	9.2
Rose	16.4	12.0	9.8	4.9	5.7	5.6	5.4
Sagebrush Fringed[1]	--	16.4	--	12.4	--	9.3	7.6
Serviceberry	18.5	13.6	12.3	6.7	6.2	6.4	7.0
Snowberry Common	13.1	6.8	10.7	4.2	5.6	5.1	5.2
Snowberry Western	18.7	11.7	10.8	5.3	6.8	4.1	4.8

[1]Current annual growth (leaves and stems combined).

may be an important factor in its high use by deer during fall and winter. Only chokecherry, fringed sagebrush (*Artemisia frigida*), and serviceberry provided the 7 percent protein level suggested by various researchers (Dietz 1965, 1970) to be minimal for deer. Fringed sagebrush, utilized mainly in the winter and early spring, was a good source of protein during those periods of preferred use. Aspen *(Populus tremuloides)*, rose *(Rosa woodsii)*, western snowberry, and common snowberry *(Symphoricarpos albus)* are principally summer-use browses, possibly because they contain rather low protein levels during the dormant season. Studies in other areas indicate the preference for big sagebrush (*Artemisia tridentata*) in late winter and early spring is due to its having higher protein levels than other species during that period (Dietz and Yeager 1959).

Apparent crude protein digestibility varies with plant maturation. As the cell wall hardens through lignification, protein and other nutrients become less easily available to rumen micro-organisms.

Crude protein digestibilities of important shrubs on a Colorado deer range reported by Dietz and others (1962a) were: big sagebrush 55.8 percent, mountain-mahogany (*Cercocarpus montanus*) 42.9 percent, and bitterbrush (*Purshia tridentata*) 30.7 percent. The low *in vivo* digestibility of bitterbrush and mountain-mahogany determined by these authors is surprising because of their recognized high preference on western deer ranges.

A factor that should be considered in addition to crude protein level and apparent crude protein digestibility of shrubs is how well animals perform when feeding upon them. If an animal assimilates enough nitrogen to satisfy the needs of the rumen micro-organisms, then higher levels are probably unnecessary. This can only be evaluated by animal performance trials where such items as weight gain, skeletal development, reproductive success, etc., are measured. However, botanical analyses of rumen contents can identify the diet of wild ruminants collected in the field, and these analyses can be correlated with various animal condition indices such as weight, kidney and bone marrow fat, and reproductive success.

Carbohydrate

Most of the plant material eaten by animals consists of some form of carbohydrate. Carbohydrates provide most of the energy for ruminant animals and furnish needed bulk in the diet. The term carbohydrate includes the simple and complex sugars, starch, cellulose, hemicellulose, gums, and related substances. Reports on carbohydrates of importance in specific shrubs are scarce, thus the following discussion pertains to trees and shrubs in general.

The simple hexose sugar, glucose, is found in plant tissues in large quantities. It occurs in cellulose and starch in condensed form. Fructose, also a simple sugar, occurs in plants but in lower concentrations. Both also occur in xylem sap of various trees. Pentose sugars are usually not found free in plants but their condensation products, the pentosans, are important cell wall constituents. Disaccharides such as sucrose are abundant in trees (Kramer and Kozlowski 1960).

Complex carbohydrates such as starch and cellulose are the most important polysaccharides in trees and shrubs. Starch is the most common reserve carbohydrate in shrubs. It is formed by condensation of glucose molecules into long spiral chains. The main components are amylopectin and amylose. Starch grains occur in sapwood and phloem cells of inner bark and leaves, but not in heartwood (Kramer and Kozlowski 1960).

Cellulose is the chief constituent of cell walls of shrubs and forms the supportive structures. Cellulose molecules consist of many glucose residues linked together in long unbranched chains. The chains form micelles, which then form microfibrils. The space between the micelles and microfibrils may be occupied by water solution in pure cellulose walls, but become partially filled with lignin in woody tissue.

Hemicelluloses occur in all woody tissues. They include arabans, xylans, galactans, and mannans. Sometimes the hemicelluloses are digested and used as reserve foods by plants. There is no general agreement on the extent to which hemicelluloses found in cell walls of woody tissue are used as reserve food. Kramer and Kozlowski (1960) state, "Many of the carbohydrates found in plants are less stable than once supposed and actually are continually undergoing conversion from one form to another or being transformed into compounds used in respiration or the synthesis of fats, proteins, and other noncarbohydrates."

Woody plants transform sugar to starch in the summer and fall, and change starch back to sugar in winter. For ruminants this probably makes little difference in nutritional value *per se* but it might have an effect on palatability and thus nutritive intake.

Simple carbohydrates translocated to meristematic regions such as stem tips are converted by an "assimilation" process into cellulose, pectic compounds, and lignin in new cell walls (Kramer and Kozlowski 1960).

Despite years of research on lignin, neither its composition nor synthesis has been completely worked out. Nevertheless knowledge of its concentrations provide useful information to the shrub nutrition researcher. Lignin concentrations increase in shrubs as plants mature. This nondigestible portion is negatively correlated with both dry matter and protein digestibility. It apparently acts as a barrier to micro-organisms attempting to attack the cellulose in the cell wall and various intracellular nutrients.

The Weende system of proximate analysis was an early attempt to devise a routine method for separating carbohydrates into digestible and nondigestible portions. In essence, this separates carbohydrates into a crude fiber portion (by empirical means) and nitrogen-free extract (NFE) by calculation (Van Soest 1966). The usefulness of this system has been questioned for some time because micro-organisms digest much of

the material designated as crude fiber and not all of that designated NFE. Much of the lignin (nondigestible) and most of the hemicellulose (partially digestible) is found in the NFE portion. Van Soest (1967) has developed a comprehensive feed analysis system using solubilities of cell contents and cell-wall constituents in neutral and acid detergents. This appears to relate more closely to actual animal performance in digesting feed material, and should prove useful in the chemical analysis of shrubs. The cell contents (protein, sugars, starch, pectin, etc.) are soluble in both neutral and acid detergent. In separation of the cell wall constituents, hemicellulose is insoluble in neutral detergent but soluble in acid detergent, while cellulose and lignin are insoluble in both neutral and acid detergent. A comparison of neutral-detergent and acid-detergent fiber provides a measure of hemicellulose, which comprises a large portion of the digestible carbohydrates in the ruminant diet (Van Soest and Wine 1967).

Acid-detergent fiber (ADF), acid-detergent lignin (ADL), and cellulose content of some important shrubs fed upon by deer in the Black Hills of South Dakota are given in table 2. With the exception of aspen and fringed sagebrush, both ADF and ADL increased markedly from spring through winter. Cellulose, ADF, and ADL were also considerably higher in stems than leaves in most instances. The increase in cellulose, ADF, and ADL with seasonal progression indicates a coinciding decrease in digestibility.

Lipids, fats, and related substances

The term crude fat (ether extract) includes a wide variety of substances soluble in certain organic solvents and insoluble in water. An abbreviated outline of lipid substances presented by Kramer and Kozlowski (1960) illustrates the wide variety of items included in crude fat. For instance, the terpenes, resins, and essential oils are extracted with ether but are not digestible to any extent, and may even inhibit rumen function (Nagy and others 1964).

The true lipids included are: simple lipids, true fats and oils, compound lipids such as phospholipides, and derived lipids such as saturated and unsaturated fatty acids. Most of these are digestible in varying degrees by ruminants. Fats serve as an important form of storage food for shrubs and as a respiratory substrate in buds, twigs, and bark. Fats are highly important reserve foods because they contain almost twice as much energy per unit of weight as carbohydrates or proteins (Kramer and Kozlowski 1960).

While the fat content may be as high as 70 percent in dry fruits and seeds of shrubs, they rarely make up more than 5 percent of the stem and/or leaf constituents. Fats tend to decrease in shrubs with seasonal progression through July, then increase in fall and winter (Dietz and others 1962b). Currently, fats are not considered to be as important in ruminant nutrition as they were formerly thought to be. The principal reason is that, as previously mentioned, the ether extract or crude fat determination includes fractions such as the nondigestible essential oils (Sullivan 1962). Big sagebrush and Rocky Mountain juniper (*Juniperus scopulorum*) contain considerable amounts of essential oils; crude fat tests on such species can give misleading results (Dietz and others 1962b). Although ruminants are not dependent upon fat in shrubs (fat is synthesized in the rumen from carbohydrates and proteins), range animals seem to do well on shrubs such as winterfat and aspen which contain good fat levels (Esplin and others 1937; Dietz and others 1962b).

Minerals

Almost all of the mineral content of plants is recovered in the ash left after ignition at 600° C. Ash gives an indication of the total mineral content, but may be misleading because of high levels of silica or other nonnutritious elements. It is often an advantage to know the ash content of forages because many measurements of digestibility (and of certain substances which relate to digestibility) are made on an ash-free basis (Sullivan 1962).

Table 2.--*Seasonal content of carbohydrate components in some important shrubs in the Black Hills of South Dakota. Ovendry basis.*

Species and component		Spring		Summer		Fall		Winter
		Leaves	Stems	Leaves	Stems	Leaves	Stems	Stems
		Percent						
Aspen	ADF	32.5	45.4	28.6	43.7	32.1	37.6	36.4
	ADL	17.9	22.0	13.1	26.0	13.3	21.2	16.4
	CELL.	15.6	18.5	14.7	21.6	15.7	19.1	15.9
Chokecherry	ADF	17.9	28.7	19.2	40.8	28.5	45.7	46.4
	ADL	7.6	6.3	6.8	16.3	12.3	22.7	25.6
	CELL.	12.3	19.7	12.6	22.8	14.7	24.2	21.0
Rose	ADF	18.3	33.6	18.1	43.5	21.4	39.1	42.8
	ADL	3.9	8.4	4.8	--	7.4	15.1	16.0
	CELL.	15.8	24.4	12.8	29.5	15.0	30.4	22.8
Sagebrush Fringed[1]	ADF		32.7		35.5		35.7	36.0
	ADL		5.3		9.3		12.1	17.4
	CELL.		29.0		24.9		24.1	25.3
Serviceberry	ADF	18.7	32.0	22.3	42.7	29.8	44.4	43.6
	ADL	7.4	6.9	9.8	15.7	15.2	19.7	20.1
	CELL.	13.2	24.8	12.2	22.0	13.3	25.6	21.0
Snowberry Common	ADF	18.3	39.1	20.1	47.8	24.4	48.7	50.0
	ADL	7.5	11.0	8.5	--	11.4	17.0	20.5
	CELL.	11.5	27.3	11.1	--	14.0	27.3	26.0
Snowberry Western	ADF	21.1	--	17.9	39.8	22.8	49.7	52.2
	ADL	8.3	--	8.4	--	10.9	18.0	21.3
	CELL.	11.9	--	19.8	26.5	11.3	34.6	26.4

ADF - Acid-detergent fiber.
ADL - Acid-detergent Lignin
CELL. - Cellulose.

[1]Current annual growth (leaves and stems combined).

The two most important minerals normally reported in routine feed analyses are calcium and phosphorus. Other minerals--such as sodium, potassium, chlorine, magnesium, iron, sulfur, iodine, manganese, copper, cobalt, and zinc--while necessary for many body processes are usually supplied in adequate amounts in common shrubs and are not normally reported in routine feed analyses. Some of these minerals function as constituents or activators of enzymes and are needed only in very small amounts (Morrison 1957).

The ruminant animal must have access to adequate calcium supplies. Calcium and phosphorus compounds comprise about 90 percent of the mineral matter in the skeletons of livestock and about 75 percent of that in their entire bodies. Half of the minerals in milk are calcium and phosphorus compounds (Morrison 1957). Low blood serum-calcium values are associated with nervous irritability, muscle spasms, convulsions, and rickets (Anderson 1953). On western ranges in the United States, calcium supplies are usually ample in shrubs and may be high enough to affect adversely the metabolism of phosphorus (Morrison 1957).

Phosphorus, vital in many body processes, is an essential part of the skeleton, intracellular fluid, and compounds such as nucleoproteins and phospholipides. It is necessary in the transfer of energy through the action of adenosine triphosphate (ATP) (Anderson 1953). A deficiency of phosphorus or a wide calcium-phosphorus ratio may cause retarded growth, weak young, decreased lactation, failure to conceive, and many other abnormalities. A desirable calcium-phosphorus ratio is somewhere between 1 to 2 and 2 to 1, but wider ratios are permissible if sufficient Vitamin D is present in the ration (Maynard and Loosli 1956).

Phosphorus is deficient in many shrub species on ranges throughout the United States during the winter season. Shrub species that maintain adequate phosphorus levels during the dormant season should be encouraged on winter ranges by various management techniques, such as proper utilization and period of use.

Seasonal ash, calcium, and phosphorus percentages contained in the leaves and stems of major shrubs fed upon by deer in the Black Hills of South Dakota are presented in table 3. Spring and summer leaves of these shrubs contained ample calcium levels, adequate phosphorus levels, and acceptable calcium-phosphorus ratios. Serviceberry, western snowberry, chokecherry, and rose leaves contained good phosphorus percentages in the spring and retained adequate levels into the fall. The stems of western snowberry and rose were below the 0.16 percent phosphorus level recommended as minimal for pregnant ewes (The National Academy of Sciences-National Research Council 1957).

The stems of chokecherry, aspen, and fringed sagebrush exceeded minimum phosphorus requirements during winter, and only rose was slightly deficient in this mineral.

Vitamins

Vitamins, organic compounds essential for normal functioning of the body, are required in only minute amounts. The vitamins vary so in structure they cannot be described by a general chemical structure and are usually characterized by physiological function. Their chemical role is largely catalytic: they usually form a part of or act with various enzymes (Peterson and Strong 1953). The oil-soluble vitamins--A, D, and E--are needed in the diet of ruminant animals, but the water-soluble vitamins--C, B complex, K, etc.--can be synthesized from other food constituents by rumen bacteria.

Vitamin A is of most importance to range ruminants because it is most likely to be deficient. Vitamin D can be obtained from sunlight and is usually not a problem for range animals. Beta carotene is the major source of Vitamin A in shrubs. Approximately 50 percent of the beta carotene in forage is converted to Vitamin A by the animal body (Anderson 1953). Vitamin A is needed in only minute amounts, but can be stored for only relatively short periods in the animal; it is needed to prevent night blindness, eye lesions, general degeneration of the nervous system, and unsuccessful reproduction (Morrison 1957).

Shrubs are usually high in carotene content during early growth, especially in developing leaves, but levels decline rapidly after maturation and dormant shrubs are often deficient. Because evergreen shrubs tend to hold up well in carotene, they are a valuable source of Vitamin A on winter ranges.

Table 3.--*Seasonal ash, calcium and phosphorus content in some important shrubs in the Black Hills of South Dakota. Ovendry basis.*

Species		Spring		Summer		Fall		Winter
		Leaves	Stems	Leaves	Stems	Leaves	Stems	Stems
		Percent						
Aspen	Ash	5.0	5.8	5.0	4.0	6.2	3.5	3.5
	Ca	0.95	0.90	1.71	1.29	2.31	1.28	1.25
	P	0.38	0.39	0.19	0.19	0.16	0.19	0.18
Chokecherry	Ash	6.1	5.5	6.6	4.2	7.5	3.7	4.2
	Ca	1.12	0.90	1.80	1.50	2.33	1.66	1.87
	P	0.51	0.41	0.39	0.21	0.37	0.21	0.19
Rose	Ash	5.9	5.4	6.2	4.3	6.1	3.0	2.9
	Ca	1.11	1.18	1.31	1.17	2.02	1.30	1.25
	P	0.48	0.32	0.30	0.15	0.29	0.11	0.12
Sagebrush, Fringed[1]	Ash		6.9		5.9		5.4	5.1
	Ca		0.71		0.72		0.84	1.01
	P		0.40		0.37		0.31	0.18
Serviceberry	Ash	6.6	5.8	6.0	4.2	5.3	3.5	3.6
	Ca	1.07	1.28	1.18	1.63	1.52	1.57	1.55
	P	0.59	0.34	0.40	0.15	0.36	0.15	0.16
Snowberry, Common	Ash	6.2	5.9	6.2	3.9	6.5	4.4	5.0
	Ca	0.82	0.90	1.21	1.17	1.70	1.31	1.27
	P	0.35	0.22	0.31	0.13	0.35	0.14	0.15
Snowberry, Western	Ash	6.7	7.3	6.3	4.3	5.9	3.8	4.1
	Ca	0.70	0.64	0.60	0.75	0.95	0.63	0.75
	P	0.56	0.41	0.39	0.20	0.43	0.10	0.15

[1]Current annual growth (leaves and stems combined).

Energy

Energy is a highly significant measure of the nutritive value of feeds. Considerably more nutrient is required to maintain normal energy metabolism than for all other purposes combined. Energy is the major basis in the compilation of diets for humans as well as of rations for livestock (Swift 1957). It is used extensively in determining the feeding value of shrub ranges. With the possible exception of protein and phosphorus deficiencies, the most common nutritional deficiency affecting range animals is lack of either available energy, digestible energy, or both. Even if abundantly available, low-quality roughage will not supply enough total digestible nutrients to meet the requirements of ruminants (The National Academy of Sciences-National Research Council 1957, 1963).

A measure of gross energy is important because it provides a common basis for expressing nutritive value. In general, fats produce more than twice as much energy-producing substance as carbohydrates, while proteins have only slightly higher energy

Table 4.--*Seasonal gross energy content in some important shrubs in the Black Hills of South Dakota. Ovendry basis.*

Species	Spring		Summer		Fall		Winter
	Leaves	Stems	Leaves	Stems	Leaves	Stems	Stems
	cal./g.						
Aspen	5,158	4,790	5,033	5,082	4,939	5,321	5,103
Chokecherry	4,879	4,623	4,886	4,651	4,689	4,841	4,713
Rose	4,542	4,476	4,792	4,581	4,557	4,693	4,637
Sagebrush, Fringed[1]		4,737		5,022		5,068	4,852
Serviceberry	4,862	4,746	4,916	4,770	4,999	4,922	4,793
Snowberry, Common	4,953	4,560	4,770	4,591	5,042	4,687	4,617
Snowberry, Western	4,973	4,590	4,915	4,757	4,917	4,635	4,376

[1]Current annual growth (leaves and stems combined).

values than carbohydrates (Maynard and Loosli 1956). Gross energy values can be misleading, especially if essential oil content is high. These nondigestible oils give off considerable heat upon combustion and indicate high energy values which are not usable by animals. To be of most use, gross energy data should be supplemented by information concerning digestible or metabolizable energy whenever possible.

Generally, browse species are good sources of energy, but some as reported by Cook and others (1954) are definitely low in energy-furnishing constituents. The deciduous shrubs such as chokecherry and serviceberry appear to provide less energy in winter than those species that retain green leaves late into the winter such as bitterbrush. The evergreen and semievergreen species such as juniper and sagebrush tend to have high gross energy values, but this is partially due to high essential oil content. Gross energy values of Black Hills shrubs (table 4) indicate aspen and fringed sagebrush to be the best sources of calories for deer in winter, although the sagebrush probably has a high essential oil content. Western snowberry, a good source of energy from spring through fall, is considerably lower in calories during winter than the other shrubs. Both the leaves and stems of aspen contain high energy levels during seasonal progression. The two snowberries contain higher levels in leaves than stems. All of the species are above 4,000 calories per gram of dry material at all seasons, indicating no gross energy deficiency on this important winter deer range. This is substantiated by the data shown in table 5. Information concerning digestible or metabolizable energy would greatly assist in evaluating the usable energy value of these shrubs.

Digestibility

Although data on the proximate composition of shrubs serve as guides in indicating their probable nutritive value, feeding trials are needed to provide a more definitive reference (King and McClure 1944). Atwood (1948) compared the gross composition of a plant to its ability to combat starvation, and concluded that a routine feed analysis alone is unreliable as an indicator of nutritive value and digestion trials are necessary. Digestion trials have shown that older, more mature, fall and winter shrub material is less readily digested than newer, tender, spring growth; thus, any protein deficiency in the fall and winter may be much greater than shown by routine chemical analysis (Biswell and others 1945).

Table 5.--*Dry matter and nutritive production of important shrubs during fall on a deer range in the Black Hills of South Dakota. Ovendry basis.*

Species	Dry matter production	Crude protein		Gross energy	
	Lbs./acre	*Percent*	*Lbs./acre*	*K cal./g.*	*K cal./acre*
Rose	25.5	5.8	1.48	4.591	53,150
Sagebrush, Fringed	23.7	9.3	2.20	5.068	54,530
Snowberry, Common	14.7	5.9	.87	4.933	32.920
Aspen	10.2	5.4	.55	5.045	23,363
Chokecherry	4.0	7.9	.32	4.787	8,694
Serviceberry	3.8	6.6	.25	4.963	8,563
Total	81.9		5.67		181,220

In vivo digestibility

The *in vivo* or classic digestion trial involved feeding known amounts of browse or other forage to animals either caged or fitted with feces collection apparatus. Chemical analyses were performed on both feed and feces to determine digestible protein and total digestible nutrients. This is a relatively accurate but very time-consuming method, and involves large expenditures for animals and feed. The collection of sufficient leaves and stems of shrubs to conduct a statistically valid number of multianimal digestion trials is an almost insurmountable barrier. Digestibility trials by *in vivo* techniques are summarized by Short (1970). Dietz and others (1962a) presented *in vivo* digestibility coefficients for deer in Colorado.

In vitro digestibility

The use of the *in vitro* technique has greatly simplified the determination of digestible dry matter. The advantages of the method are that large numbers of samples can be digested simultaneouly with rumen fluid from one or more animals, and thus are reasonably comparable. A disadvantage is that only digestible dry matter or cellulose is usually determined, thus no information on the digestibility of individual nutrients is obtained. In review of *in vitro* digestibility trials, Pearson (1970) recommends that *in vitro* measurements are most useful when compared directly with animal performance rather than with *in vivo* determinations.

Mean dry matter digestion coefficients of shrubs on a Black Hills deer range were determined by the *in vitro* method using rumen fluid of white-tailed deer (table 6). Common snowberry was the most digestible shrub during the spring, followed closely by rose. Chokecherry also exhibited good digestibility during the early growing season. Fringed sagebrush and aspen had the best dry-matter digestibilities during the winter

when the shrubs were dormant. The low dry-matter digestibility of aspen and fringed sagebrush in the spring coincided with high acid-detergent fiber content (table 2). The low digestibility of the snowberries during winter could have been predicted by the high acid-detergent lignin and acid-detergent fiber content of those species during that season.

Volatile fatty acids

Another phase of *in vitro* digestibility is the determination of volatile fatty acids (VFA). The principal sources of energy for the ruminant are lactic acid and volatile fatty acids produced in the rumen (Annison and Lewis 1959). The major volatile fatty acids, listed by Church (1969) in order of molar percentages normally found in rumens of range animals, are: acetic 60-67 percent; propionic 18-23 percent; butyric 12-15 percent; valeric 0-1.7 percent; and other 0-4 percent.

There have been several studies on VFA content of rumen material collected from deer fed shrubs (Ullrey and others 1964; 1970), and from deer feeding on shrub ranges (Short and others 1966b).

Ullrey and associates (1964) reported that white-tailed deer fed cedar had higher volatile fatty acid concentrations in the rumen liquor than those fed aspen. Short and others (1966b) found that the proportion of volatile fatty acids in deer rumino-reticular contents changed significantly from the fall and winter period to the spring and summer period. Because volatile fatty acids may account for as much as 75 percent of the energy needed for maintenance of ruminant animals, the usefulness of VFA techniques for studying the nutritional value of shrub ranges is quite evident (Shaw 1959).

Nutrient production

Knowledge of dry-matter production of shrubs or other plant material on rangelands is no longer sufficient in itself to achieve the needed level of expertise to arrive at effective management decisions (Burdick 1957). We are now in a position to improve and refine carrying capacity estimates for livestock and big game ruminants by the marriage of dry-matter and nutrient-production data with digestibility information. Data on usable nutrient production per unit area, when evaluated in the light of animal nutrient requirements, provide the range manager an effective tool in the proper allocation and manipulation of range resources.

In a current study on a key winter deer range in the Black Hills of South Dakota, an attempt is being made to refine carrying capacity estimates. The first step was a botanical analysis of deer rumen contents collected periodically during the year. This was important in establishing the seasonal diet of deer, and permitted the selection of important dietary components for further study. The second step involved determining dry-matter production in weight per unit area (table 5). *In vitro* digestible dry matter was determined for each species using rumen juice from deer collected on the study area (table 6). Comparing daily requirements of nutrient factors for deer with nutrients produced on the range as shown in table 7 permitted a prediction of carrying capacity based on each factor. Data in table 7 indicate that crude protein production is the limiting factor for deer on this range, rather than digestible dry matter or gross energy. Rose was the greatest producer of dry matter, but because of lower digestibility and crude protein content, will probably not support as many deer per unit area as fringed sagebrush. One important factor not evaluated was the contribution of grasses and forbs to the nutritive regime. All food components must be considered before carrying capacity of deer range can be predicted realistically.

Table 6.--*Digestible dry matter content of some important shrubs in the Black Hills of South Dakota determined with white-tailed deer.* In vitro *method, ovendry basis.*

Species	Season	
	Spring[1]	Winter[2]
	Percent	
Aspen	44.5	57.4
Chokecherry	56.9	51.3
Rose	65.9	54.5
Sagebrush, Fringed	45.0	59.5
Serviceberry	48.1	54.4
Snowberry, Common	71.4	41.3
Snowberry, Western	--	41.0

[1]Samples in early leaf stage.
[2]Samples in dormant stage.

Table 7.--*Predicted maximum deer range carrying capacity during the dormant season based on production of dry matter, digestible dry matter, crude protein and gross energy of some Black Hills shrubs (Reduce by one-half for moderate 50% use of annual growth).*

Species	Dry matter	Digestible dry matter	Crude protein	Gross energy
	Deer days/Acre			
Rose	6.4	7.0	5.3	8.4
Sagebrush, Fringed	5.9	7.1	7.9	8.7
Snowberry, Common	3.7	3.1	3.1	5.2
Aspen	2.6	3.0	2.0	3.7
Chokecherry	1.0	1.1	1.1	1.4
Serviceberry	1.0	1.1	.9	1.4
Total	20.6	22.4	20.3	28.8
Daily requirement per cwt. of deer	4 lb.	2 lb.	.28 lb.	6,300 K cal.

Conclusions and summary

Shrubs are important sources of nutrients for most classes of domestic and wild herbivores, especially during the winter season. New concepts and techniques in determining the nutritive value of shrubs on wildland ranges are greatly adding to our understanding of the nutritional relationships between shrubs and range animals.

Many shrub species are good sources of crude protein. Ruminant animals synthesize protein from nitrogen compounds in plants. Protein is one of the most important nutrients to animals because of its profound effect on energy relationships and metabolic processes in general.

Carbohydrates make up the largest component of the leaves and stems of shrubs, and are the principal source of energy for ruminants. The soluble carbohydrates such as sugars and starches are found inside the plant cell along with nitrogen and other minerals, while the more insoluble materials such as cellulose, hemicellulose, and lignin are contained in the cell wall. Shrubs are highly digestible during periods of plant growth but become more difficult to digest as the cell walls become lignified. Stems contain higher percentages of fiber, cellulose, and lignin than leaves. Percentages of these components increase in leaves as the shrubs mature.

Mineral content of plants vary with species, plant part, and season. Calcium supplies are usually adequate in shrubs, but phosphorus levels often are deficient during the dormant season; wide calcium-phosphorus ratios occur, to the detriment of browsing animals.

Laboratory tests for crude protein, fiber, cellulose, lignin, and *in vitro* digestible dry matter enable the range nutritionist to estimate digestible protein and carbohydrate available to range ruminants during various periods of the year. When this information is combined with dry-matter production and then compared to daily dietary requirements of animals, range carrying capacity can be estimated. Animal use of shrubs must be managed in such a way that the plants retain sufficient nutrients for their own physiological processes, while furnishing adequate nutrients for browsing animals.

Comparative nutritive values of forbs, grasses and shrubs

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The quality of a range plant is judged primarily upon how readily it is eaten by animals and its nutritive content with respect to its phenological development. Some plant species are eaten only during early growth and, in special cases, only certain portions of a particular species are consumed during the latter stages of development.

During their annual life cycles, individual plant species vary materially in nutrient content. Most forage plants are high in nutrients during early growth. However, as they mature they lose nutrients markedly. Some plant species mature rather rapidly and as a result decrease substantially in nutritional value; other species mature rather slowly and consequently remain high in nutrient content over an extended period. Still other plant species, even after they mature, appear to cure rather well and retain comparatively high quantities of nutrients over indefinite periods.

The true test of the nutrient value of a forage species, or a mixture of species, is the ability of the usable forage to meet the nutritional requirement for the physiological function being performed by the grazing animal during the various seasons of the year. Most physiological functions of the grazing animal are performed as everyday functions and are generally referred to as "maintenance requirements" which include travel, mastication, digestion, maintaining body temperature, and growing of hair or wool.

Of the three forage classes, shrubby species, in most cases, contain higher levels of lignin, phosphorus, calcium, and protein. Grasses are higher in crude fiber, cellulose, and gross energy. In most cases, forbs are intermediate between browse and grasses in chemical content (Cook 1971; Cook and Harris 1968). The nutrient evaluation of most range areas can be based on how much protein, energy, phosphorus, and carotene are in the forage plants.

The comparative nutritive value among the forage classes (browse, forbs, and grasses) can best be discussed by measuring their apparent ability to meet the nutritional requirements of large herbivores for the more important physiological functions.

In addition to the influence of relative preference and floristic composition on nutritive content of range forage, there are other important factors such as stage of growth and variable site conditions.

Nutritional content and stage of growth

During the period of initial growth and, for a time thereafter, all forage classes are high in nutrient content, and their nutritional contents are not materially different. However, as growth stages advance, the nutritional differences among forage classes become more evident (figs. 1 through 4).

It is a common belief that animals grazing green plant growth on spring and summer range receive adequate nutrients; however, on fall and winter range where plants are dry and mature, the diets of grazing animals are thought to be deficient in some nutrients.

Several studies have shown that chemical composition varies with season largely as a result of change in the stem-to-leaf ratio and the normal maturing process that causes a translocation of nutrients within the plant parts (Fagan and Milton 1931; Cook and others 1956). In addition to the actual decrease in chemical content of herbage with advancement of growth, the forage likewise decreases in digestibility because of lignification and calcification of the plant material.

Carotene

Browse species decrease only slightly in carotene content from early growth to maturity (fig. 1) because of the high carotene content in the covering of bark on young twigs. Grasses lose their carotene rather rapidly during advanced stages of maturity and contain almost none after they turn straw-colored during quiescence. Carotene content places forbs in an intermediate position between browse and grass, but forbs generally contain only a small amount of carotene by the time the leaves are lost and the stems are dry and dormant.

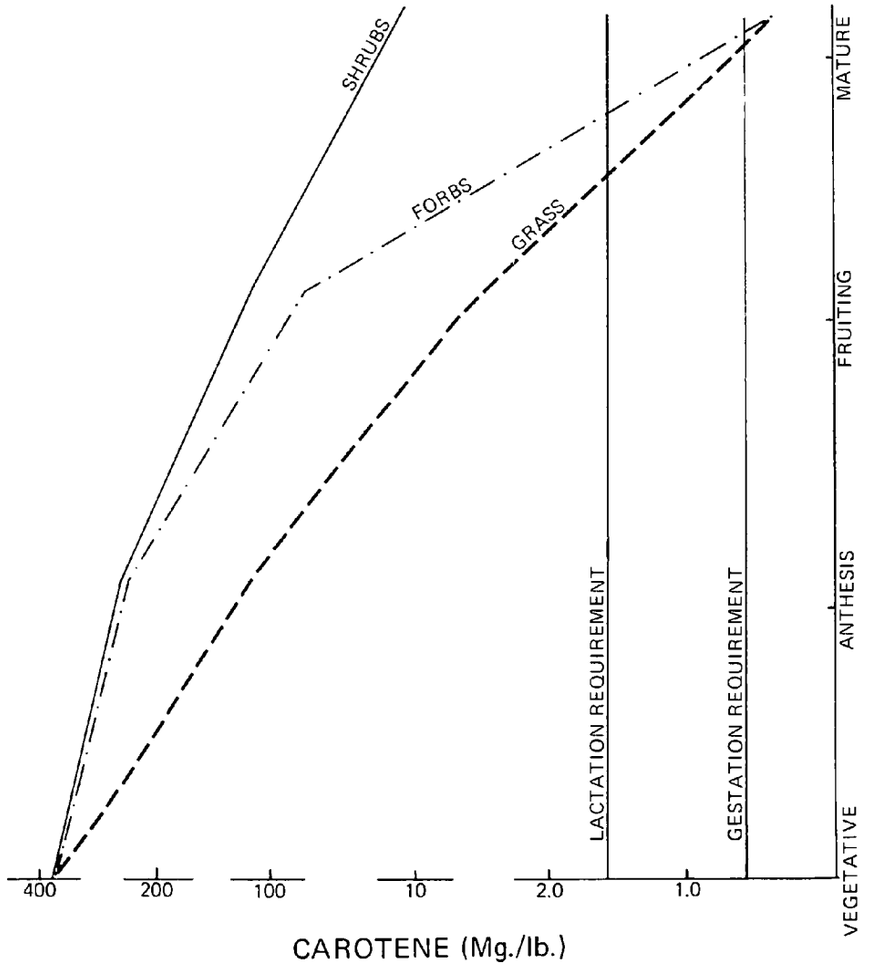

Figure 1.--Average carotene content of the three forage classes compared to phenological stage of development and requirements for lactation and gestation.

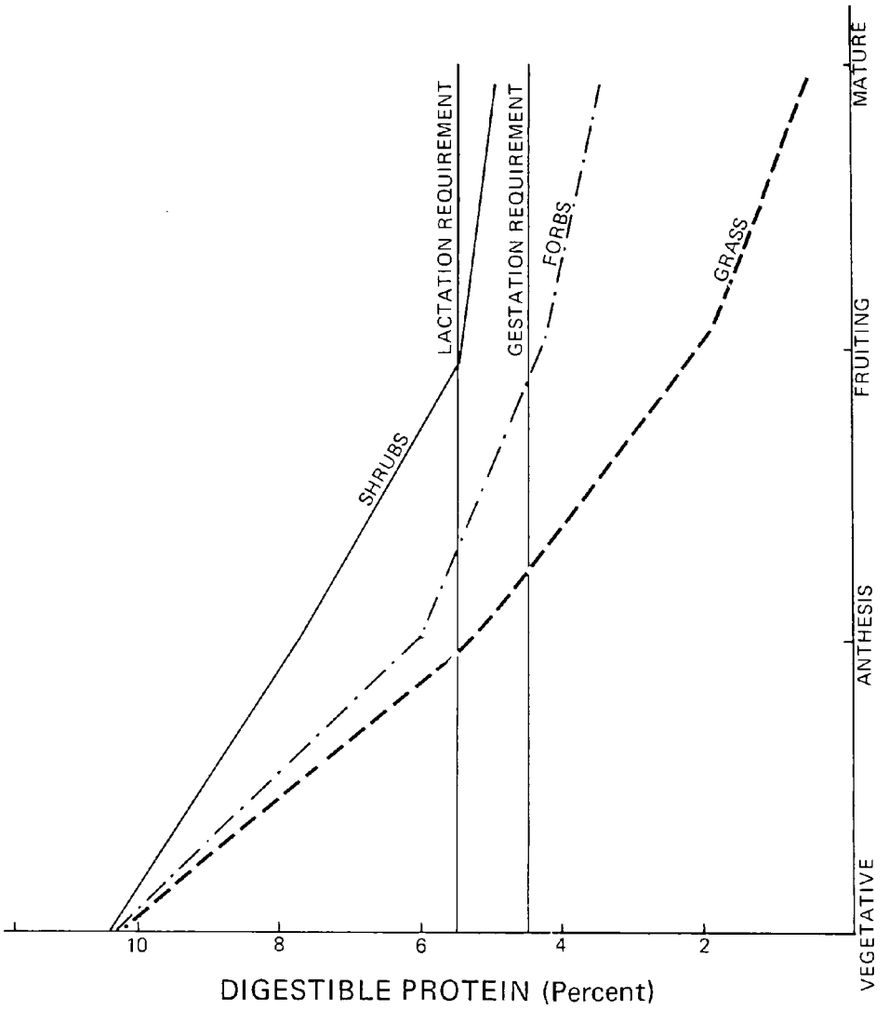

Figure 2.--Average content of digestible protein for the three forage classes, compared to phenological development and herbivore requirements for lactation and gestation.

Browse species in all stages of growth furnish enough carotene to meet the vitamin A requirements for even lactating or growing animals. However, species of grass and forbs, when mature, fail to furnish even the minimum requirements of vitamin A for gestating animals.

Digestible protein

There is a rather high correlation between total protein and digestible protein in the mixed ration normally used in farmstead feeding. In range forages the digestibility of protein may vary from 70 percent in early growth to as low as 10 to 15 percent in the quiescent stages. It thus appears more logical to evaluate the grazing animals' diet on the basis of digestible protein rather than on total protein unless standards have considered the high variability in digestibility of protein as plants mature.

Grass species decline in digestible protein rather rapidly and generally fail to meet the lactation requirements at about the time they come into full anthesis (fig. 2). This is the result of a rather rapid loss of total protein and a more rapid decrease in digestibility of protein that occurs with advanced growth. Grasses, in general, lose about 75 percent of their protein during the period from early growth to seed formation; on the other hand, browse lose only about 40 percent of their protein content during a similar period. As a result, grasses that have matured are considered poor sources of digestible protein. Shrubs, however, are considered good sources of digestible protein during most of their active growing period; and even after they reach full maturity they continue to meet gestation requirements.

Forbs are intermediate between browse and grass with respect to protein content during most seasons. Most forb species fail to furnish adequate digestible protein to meet the requirements of animal gestation after reaching the fruiting stage.

Phosphorus

Even when mature, shrubs are generally considered good sources of phosphorus for general animal maintenance and gestation, unless they are deciduous. Even deciduous shrubs are perhaps only borderline if the young twigs are readily eaten (fig. 3). Most forbs have a phosphorus content that is only slightly lower than that of shrubs. Grasses, however, are low in phosphorus soon after they form seed; so they are considered poor sources of phosphorus during quiescence. Most grasses lose considerable phosphorus content when temporarily forced into dormancy by even brief periods of drought. However, when precipitation occurs and growth is renewed, the phosphorus content increases and lactation requirements are again met.

Energy

In some cases, neither gross energy nor digestible energy in shrubs is considered a good index to the true energy values of forage because of the high content of essential oils, resins, or waxes that suggest high energy content; but these materials are not available for livestock metabolism (Cook and Harris 1968). The digestible energy values for browse shown in figure 4 have been adjusted for species high in essential oils so that the trends are based on realistic digestible energy values. Shrubs are not considered good sources of energy after they reach the phenological stage of fruit development. Thereafter, they generally fail to meet the energy requirement for animals in gestation.

Grasses are generally considered good or excellent sources of energy primarily because of their high content of cellulose. Even when they reach maturity, grasses seldom cease to furnish the energy requirements for lactation. Forbs are intermediate between shrubs and grass in energy-furnishing constituents and like shrubs, they generally fail to meet the energy requirements for gestation after reaching full maturity and dormancy.

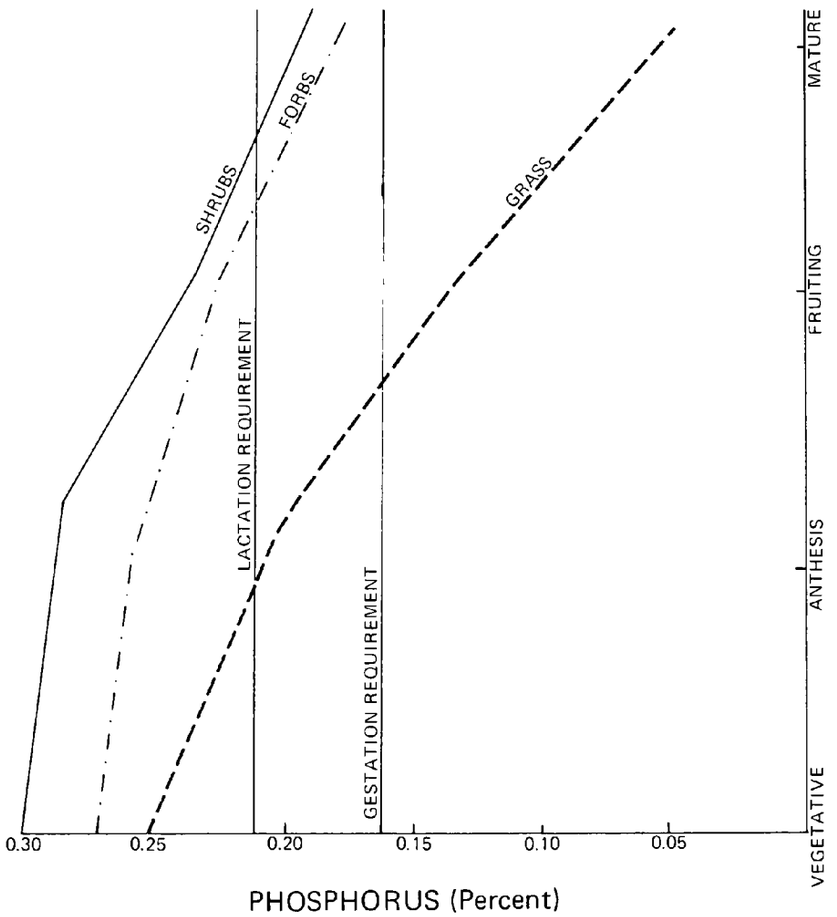

Figure 3.--Average percent phosphorus for three forage classes compared to stage of growth and herbivore requirements for lactation and gestation.

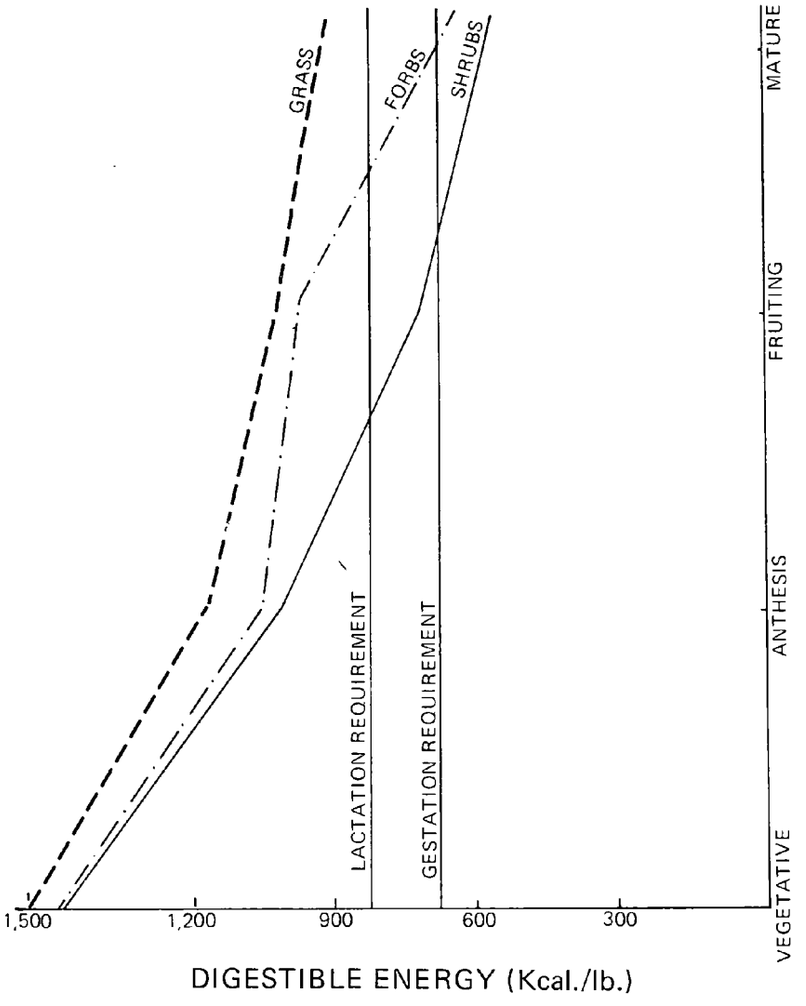

Figure 4.--Average content of digestible energy for three forage classes compared to various stages of phenological development and requirements for lactation and gestation.

Seasonal ranges and forage classes

In the Intermountain area of the West, ranges are identified with the season that apparently best suits their forage producing qualities. High mountain range is used during the summer; foothills are used during spring; and the desert basin areas are used primarily during winter. Normally, grazing animals bear their young and are in lactation during spring and summer. During the winter grazing period, range forage is expected to meet the gestation requirements. Animals may be grazed year-round in essentially the same locality in the grassland types of the Southwest and the Great Plains where lactation begins with new growth in the spring and continues throughout the summer. On most grassland ranges, gestation requirements are met by intermittent farmstead feeding periods or by giving supplements to the grazing animals while they are on the dormant ranges.

Spring ranges

The early growth of forage plants on spring ranges results in a high nutritive content; but as discussed previously, the percentage of nutrients decreases as the growth stages advance. Cool-weather grasses start growth early but lose nutrients rather rapidly, even during active growth. Warm-weather grasses start growth later in the season than cool-weather grasses, but the former retain their nutrients much better as the season advances.

Generally, all forage classes furnish rather large quantities of carotene on spring range, but some grasses and forbs may fail to furnish adequate quantities of digestible protein for lactating animals when plants reach late anthesis in late spring. Grasses

may not meet the phosphorus requirement for lactating animals during late growth stages during spring grazing, but browse and forbs generally do not become deficient until at least full maturity is reached late in the spring.

Both forbs and shrubs may become decidedly deficient in energy-furnishing constituents for lactating animals when plants approach maturity during late spring, but grasses continue to furnish adequate energy for lactating animals during the entire spring grazing season. Therefore, a stand of mixed vegetation that includes all forage classes generally meets lactating requirements for livestock throughout the entire spring grazing season.

Summer ranges

On mountain ranges where mountain brush, aspen, and coniferous types prevail, the vegetation is still in the initial growth stages even by late June or the first of July. Whereas, on the grassland plains used for summer grazing, many forage species are in rather advanced stages of growth by July 1. Intermittent precipitation, when it falls on the grassland plains area, produces renewed growth and thus increases the nutritional value. In both the mountainous areas and the grassland plains, drought periods may produce temporary dormancy in herbage and consequently produce reduced percentages of nutrient content.

On either mountain or grassland summer ranges, the plants may reach full maturity late in the season, and nutrient requirements may become borderline for growing and lactating animals.

As discussed previously, each of the three forage classes displays characteristic changes in nutrient content as advanced stages of growth occur. Late in the summer, grasses would be expected to be low in protein and phosphorus, but they would remain high in energy-yielding constituents. Shrubs, on the other hand, would remain rather high in protein and phosphorus, but they would be low in energy. Forbs, as previously stated, would be intermediate between grasses and browse in these respects. During the summer grazing season, grasses may lose considerable quantities of their protein content and increase decidedly in lignin and cellulose. Protein content of forbs and shrubs generally decreases only slightly during the summer, while lignin and cellulose content increase moderately as the season advances.

Shrubs and forbs furnish ample protein and phosphorus for growth and lactation until (at least) late in the summer grazing season unless drought conditions force plants to become dry and dormant before they normally complete their annual cycle. However, a diet composed largely of forbs and browse late in the summer might be deficient in the constituents that supply energy. Most grasses would furnish adequate energy for growing and lactating animals even late into the summer grazing season, but grasses would be deficient in both protein and phosphorus when they reached the advanced stages of growth. All three forage classes are comparatively high in carotene (vitamin A) during the entire summer grazing season unless the herbage becomes extremely dry as a result of an extended drought period.

Seasonal changes in nutrient content on summer ranges show generally that phosphorus, protein, gross energy, and carotene decrease in all three forage classes as the season advances. Grasses change the most as to nutrient content: shrubs change the least, except for changes in digestible energy. As would then be expected, browse has the highest protein and phosphorus content throughout the summer grazing season, and grasses have the highest energy content. These changes that occur with advancement of the summer grazing season are affected by changes both in the stem-leaf ratio and in chemical content of the plant parts themselves. Leaves for all forage classes are higher in ether extract, protein, phosphorus, and calcium; and stems are higher in lignin and cellulose.

Thus, it is concluded that summer ranges, including both warm- and cool-weather grasses and more than one forage class, more nearly meet growth and lactation requirements than ranges on which there is a restricted diversity in forage species.

Winter ranges

During winter on desert ranges, shrubs generally meet the gestation requirements for livestock as to protein and carotene, but they are borderline in phosphorus and are decidedly low in energy for animal metabolism. During winter the grasses are decidedly deficient in protein, carotene, and phosphorus but are good sources of energy. The broad general class of shrubs on desert ranges can be divided into two groups. The first group would include species that possess a woody base but, for the most part, have herbaceous stem growth. These are known as "suffrutescent" species. The second group includes the true shrubs, or frutescent species. The species of the second group include woody-stemmed plants of low stature. As might be expected, the suffrutescent species are intermediate between shrubs (frutescent species) and grasses in nutrient content (table 1). The suffrutescent species are slightly lower than the shrubs in these respects. In the suffrutescent species, energy-furnishing constituents are somewhat lower than in grasses but these species provide somewhat higher energy sources than browse. Again, it is suggested that a mix of forage classes in the diet is conducive to a balanced nutritional diet for grazing animals on desert ranges during the winter.

During spring while they are growing, desert shrubs are as high in nutrient content as mountainous shrubby species during comparable phenological growth stages. This is also true for grasses and forbs, but forbs are sparse on most desert ranges and therefore are not important in the diet of grazing animals. Even though desert plants are high in nutrients during growth, they can withstand only about one-half the degree of defoliation that is tolerated by mountainous and plains plants during growth (Cook 1971).

Table 1.--*Average chemical content for three shrubs, two suffrutescent, and two grass species harvested during four seasons at three intensities during 1968 (the sixth year of treatment)*

Forage class[1]	Protein	Lignin	Gross energy	Phosphorus
	Percent	*Percent*	*Mcal./kg.*[2]	*Percent*
Shrubs	11.2	12.7	3.85	0.12
Suffrutescent	10.1	9.7	3.90	.10
Grass	6.2	5.7	4.11	.09

[1]Shrubs were big sagebrush; suffrutescent species were winter fat and Nuttall's saltbush; and grasses were Indian ricegrass and squirreltail grass.

[2]Adjusted for essential oils.

Nutritive value as affected by site

Site conditions are important because they influence the growth characteristics of range plants and thus indirectly affect their nutritive value (Cook and Harris 1950). Sites also indirectly affect the chemical content of plants and plant parts through soil and plant development, water runoff, intensity of shade, and other environmental factors.

Shrubs and forbs, when they approach maturity, are considerably more leafy on less favorable growing sites. Grasses in advanced stages of growth are, likewise, more leafy on poorer sites than on more favorable sites but differences between sites are less conspicuous for grasses than for either shrubs or forbs. As a result, plants on unfavorable sites are more palatable and are more nutritious than plants on the more favorable sites (Cook and Harris 1950; Cook 1959).

Nutrient content of plants on poor sites during advanced growth stages are generally considered more nutritious because of the finer material and the presence of more leafy material compared to stems. The difference in stem-to-leaf ratios would, to a large degree, account for chemical differences between plants growing on favorable and unfavorable sites since leaves are higher in ether extract, protein, ash, calcium, phosphorus, and nitrogen-free-extract; whereas stems are higher in lignin, crude fiber, and cellulose.

Factors affecting nutritive values

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Many edaphic, climatic, and genetic factors that appreciably affect the morphology and metabolism of shrubs also affect the digestibility of shrub tissues. We substantiate this generalization in this paper with a literature survey and with data collected during 1970-71 at Nacogdoches, Texas, using the nylon bag technique (Harris and others 1967) and ruminally cannulated goats.

In this paper, shrubs are defined as low woody plants that usually have several vertical stems. Thus, some tree species whose morphologies in east Texas fit this description are treated herein as shrubs. In addition, we have cited references to tree morphology and wood chemistry when pertinent to the subject of this paper and if comparable references to shrubs were not available.

Twigs

Growth stage

Most woody plants in temperate zones produce annual shoots only from the bursting and expansion of dormant buds (Kozlowski 1964). The extent of shoot growth is dependent on bud size and is related to growing conditions during the previous year, when the buds were formed (Kozlowski 1964). Twigs of many shrub species elongate rapidly only during a relatively brief portion of the frost-free season (Halls and Alcaniz 1965).

Nutrient quality of current twigs varies directly with growth stage (Blair and Halls 1968). Relative digestibility is clearly affected by the changing nutrient quality associated with phenological change (fig. 1). In the terminal 4-inch segments of current American beautyberry *(Callicarpa americana)* twigs, for example, dry matter content, cell wall content (CWC) of green tissue, and crude protein in ovendried tissue change seasonally with growth stage (fig. 1). Very rapid growth occurs from April through early June, when current twigs are succulent and relatively low in fibrous components. Cell wall content and other fibrous constituents reach high levels by early August (Short and Harrell 1969), when twig elongation has essentially ceased. *In vivo* microdigestion of terminal 2-inch segments of current American beautyberry twigs indicates that succulent and rapidly elongating twigs are 85-percent digestible in late April. Beautyberry twigs were only about 40-percent digestible after early August, when stem elongation was complete.

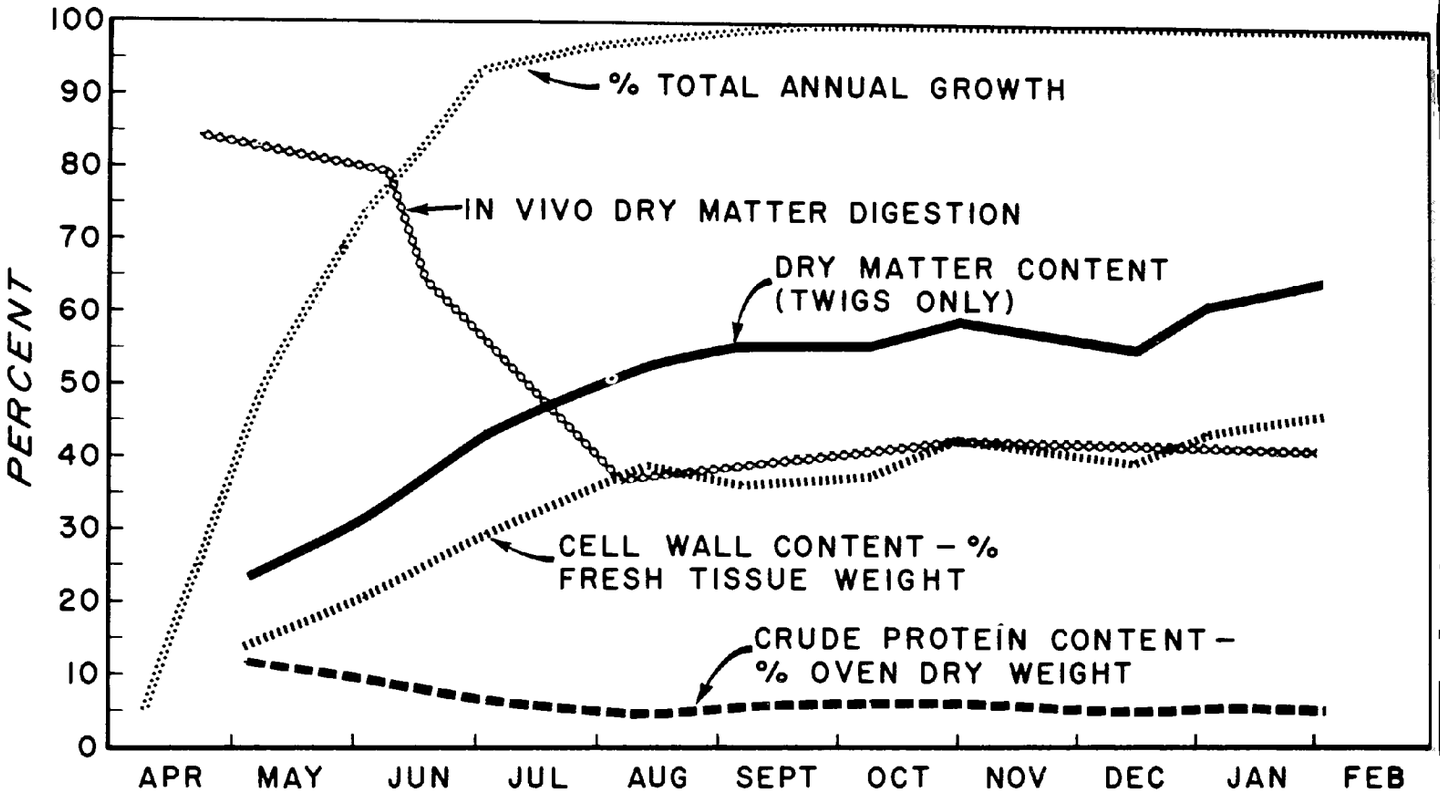

Figure 1.--In vivo *digestibility and the nutrient content of current terminal twigs of American beautyberry are related to the degree of total twig elongation. Growth curve from data in Halls and Alcaniz (1972).*

The digestibility of terminal portions of twigs changes abruptly when twig elongation nears completion (fig. 2). Twigs collected about June 8 were more digestible than those collected later in June, even though dry matter content varied little. The rapid decline in digestibility of twig tissues seems related to changes in cell structure. Woody cells are large, have large lumens, and are very digestible early in the growing season when the rate of stem elongation is rapid and auxin gradients are high (Larson 1962). As the cells grow, the cellulosic primary cell wall (cambial cell wall) increases in area. The secondary cell wall forms later and tends to increase in thickness and eventually contains some lignin (Isenberg 1963). Digestibility and nutrient quality of woody cells diminish as cells mature because cell walls thicken and become lignified (Wort 1962) and cellular protoplasm is lost.

In some woody species, shoots elongate late in the growing season from buds of the current year. Lammas shoots result from the bursting and elongation of terminal buds and proleptic shoots from the development of lateral buds. Shoots that evolve late in the season are also succulent and highly digestible only during their early development.

Environment

Conditions such as shading, water and mineral availability in the soil, topography, climate, recent fire, and plant competition affect growth of woody plants (Kozlowski 1964). Changes in nutrient composition and cell wall structure change the digestibility of shrub tissues.

Repeated burning for pine culture in east Texas retards growth of sassafras *(Sassafras albidum)* and its form is frequently shrublike with multiple stems. Current sassafras twigs were collected in September 1970 from areas that had been prescribed

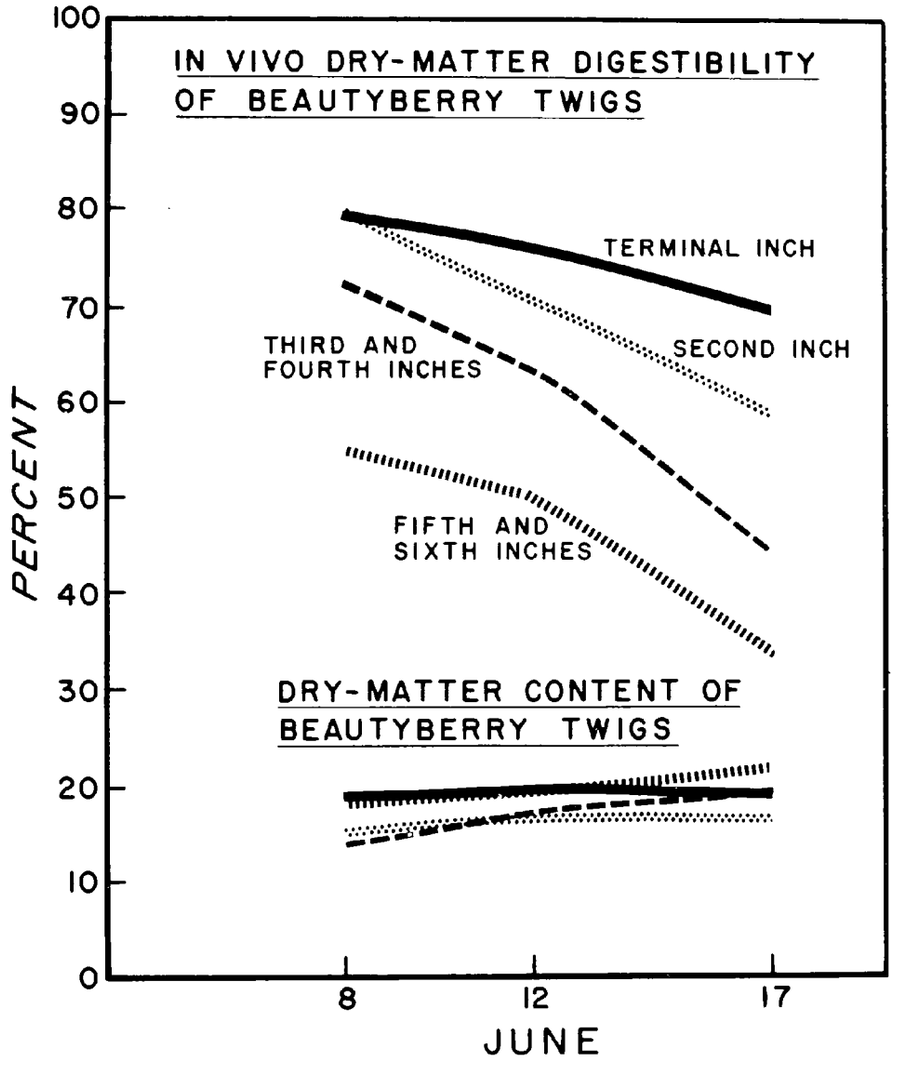

Figure 2.--Digestibility and dry matter content of four segments of current woody twigs of American beautyberry collected in mid-June when twig elongation was nearing completion.

burned in February and areas that had not been burned in more than 3 years. Comparable twig segments obtained from the recently burned sites were significantly more digestible than were segments from the nonburned sites (table 1), because of differences in the cell wall components of the two samples. For example, the lignin content of woody twigs from burned sites is diminished (table 2). The protein (DeWitt and Derby 1955; Shafer 1965; Hanson and Smith 1970) and phosphorus (Lay 1957) contents of shrub tissues are enhanced by burning.

Consecutive twig segments of sassafras from burned and unburned sites as well as those of American beautyberry (fig. 2) varied in digestibility. Terminal segments are more digestible than those with older, more distal tissue largely because of differences in cell-wall components. Lignin and cellulose contents of woody twig segments increase distally from the apex. Cowan and others (1970) found that cellulose digestion and crude protein content of twig segments of red maple *(Acer rubrum)* and black cherry *(Prunus serotina)* diminished distally from the shoot apex as cellulose content increased.

Suppression sometimes reduces the nutrient quality of woody twigs. Halls and Epps (1969) showed that nutrient quality of several shrub species was greater in the open than under a pine overstory of about 70 ft.^{2} basal area. Suppression sometimes reduces bud vigor and auxin synthesis so that the diminished cambial activity throughout the plant affects physical appearance (Larson 1962). Reduced cambial activity may affect earlywood:latewood ratios in softwoods so that suppressed pines or those from poorer sites contain higher carbohydrate:lignin ratios than do dominant pines or those from more favorable sites (Burkart and Watterston 1968). If suppression also modifies the cell wall components of shrubs, the relative digestibility of shrub tissue will be affected.

Table 1.--In vivo *dry matter digestibility of sassafras twigs and leaves collected in September from burned and unburned sites near Nacogdoches*

Material	Burned	Unburned
	Percent	
Current Twigs		
Terminal Inch	[1]48.0[a]	42.4[b]
Second "	41.4[b]	36.8[c]
Third "	38.6[c]	33.5[d]
Fourth "	31.8[d]	27.6[e]
Fifth "	31.1[d]	27.0[e]
Sixth "	28.4[e]	24.1[f]
Leaves		
Terminal & Second Inches	70.6[h]	64.7[i]
Third - Sixth "	71.6[h]	65.5[i]

[1]Twig or leaf values with the same superscript letters are not significantly different ($P < 0.05$).

Lignin

The relationship between lignin content and digestibility is different in woody tissues than in herbages. Pew and Weyna (1962) concluded that lignin protects wood carbohydrates better than alfalfa carbohydrates. Forage analyses applied to shrub tissues indicate that lignin:cell wall content ratios in current shrub twigs (Short and Harrell 1969) are greater than ratios common for grasses and legumes (Van Soest 1964). In addition, the digestible amount of CWC seems a different function of total CWC of twigs than of herbages (Short and Reagor 1970).

Current twigs of American beautyberry and sassafras, after the cessation of stem elongation, are 30- to 40 percent digestible (see fig. 1 and table 1). These values are averages representing both highly digestible inner bark tissues and relatively indigestible woody tissues. To illustrate these differential digestibilities, we collected 6-inch sassafras twigs from burned and unburned sites during November. We then separated the terminal and second 3-inch portions and peeled off the bark from each twig segment. Dry matter digestibility of sassafras bark was three to four times greater than sassafras wood (table 2). Relatively high concentrations of easily solubilized materials such as the benzene-alcohol extractives (fats, fatty acids, resins, waxes, and pigment) and cold water extractives (organic salts, simple sugars, gums, pectinlike materials and some complex polysaccharides) in bark partially account for this high digestibility.

Structural cell wall components account for about 90 percent of the dry matter of wood and 70 percent of the dry matter of bark. The digestibility of extracted bark samples was four to six times greater than that of extracted wood samples. The difference in digestibility is largely related to the lignin:carbohydrate associations in the two types of tissue.

The lignin:carbohydrate relationship in wood is incompletely understood. Apparently, neither hydrogen bonding nor chemical bonding completely explain the extensive

Table 2.--*Percent composition and digestibility of wood and bark tissues from sassafras twigs*[1]

Characteristic	Wood				Bark			
	Terminal 1-3 in.		Terminal 4-6 in.		Terminal 1-3 in.		Terminal 4-6 in.	
	Burn	Unburned	Burn	Unburned	Burn	Unburned	Burn	Unburned
Composition								
Ash	1.5	1.2	1.0	0.9	2.5	2.3	2.3	2.2
Benzene-ROH Extract	3.8	4.2	3.8	4.2	14.5	19.1	18.4	14.8
Cold Water Extract	4.2	4.3	5.8	2.7	14.6	11.4	10.0	10.7
Lignin	12.9	19.7	15.7	20.3	17.7	19.0	17.8	19.9
α-cellulose	35.5	34.4	37.9	37.9	25.4	27.4	27.3	31.5
Noncellulosic polysaccharides (Hemicelluloses)	42.1	36.2	35.8	34.0	25.3	20.8	24.2	20.9
Digestibility								
Dry matter	18.7	15.5	16.3	9.8	60.1	58.7	54.6	47.5
Extracted samples	13.9	8.9	9.3	5.9	49.8	45.0	41.0	34.2
Delignified extracted samples	74.5	78.9	68.1	83.0	72.8	66.7	68.1	69.2

[1]Samples collected in November near Nacogdoches from soils classified as Kalmia fine sandy loam.

resistance of wood to cellulolytic enzymes (Pew and Weyna 1962). Presumably, carbohydrates in the cell walls of wood tissues are surrounded by a three-dimensional network of lignin which acts as a barrier against cellulolytic enzymes and strengthens the wood fiber. The quantity, chemical nature, and distribution of lignin in wood cell walls varies by plant species (Millett and others 1970). Thus, different chemical and physical pretreatments render woody tissues of different species variously susceptible to attack by rumen micro-organisms (Tarkow and Feist 1968; Feist and others 1970; Millett and others 1970).

Lignin in bark is chemically bonded to carbohydrates and differs in composition from lignin in wood (Jensen and others 1963). Lignin may not protect carbohydrates in bark as efficiently as in wood. Thus, when the lignin is removed, digestibility of wood fibers is increased significantly more than is the digestibility of bark fibers (table 2). Delignified sassafras was 67- to 83-percent digestible, indicating that the tissue carbohydrates (α-cellulose and hemicelluloses) were very susceptible to micro-organism attack.

Inner bark and cambial tissues in current twigs have considerable nutritional significance. Inner bark contains more minerals than do woody tissues, and it stores sugars and water soluble proteins during the winter. Many tree barks contain readily solubilized carbohydrates and fatty substances (Millett and others 1970).

Some mature bark may have adverse nutritional characteristics. Aspen bark was a poor-quality roughage in nutritional trials (Enzmann and others 1969), and some bark extractives have antimicrobial properties which adversely affect *in vitro* cellulose digestion (Prins and Geelen 1968). Whereas large herbivores eat distal portions of current twigs or sapwood of trees (Radwan 1969), many smaller herbivores, such as the porcupine (Johnson and McBee 1967), squirrels (Smith 1968), beaver (Aleksiuk and Cowan 1969), and several species of mice select inner bark and cambium tissue of relatively high nutrient quality.

Leaves

Growth stage

Leaves develop as lateral protuberances on the bud apical meristem. After the bud bursts, the leaf primordia grow rapidly through cell division and enlargement. Much of the leaf consists of mesophyll cells that are thin walled, loosely arranged, and actively involved in photosynthesis. Forage analyses applied to American beautyberry tissue indicate that in comparison to twigs, leaves are more succulent and higher in crude protein, crude fat, ash, nitrogen-free extract, and cell contents but lower in crude fiber, cell wall contents, acid detergent fiber, lignin, and cellulose (table 3). Foliar nutrient content varies with age of the leaf (Blair and Epps 1967), position within the crown, time of day, and season of the year (Lowry and Avard 1965). Levels of Al, Mn, Ca, P, Mg, Bo, N, and K are greater in leaves than in either the wood or bark of small branches of many trees (Young and Guinn 1966). This difference probably also exists in woody shrubs.

Leaves of woody plants are frequently well digested by herbivores. For example, digestion trials indicate that young gular leaves (*Ficus glomerata*) are palatable, digestible, and superior to some common grasses (Majumdar and Momin 1960). On the other hand, pipal leaves (*F. religiosa*) only provided a maintenance diet (Mia and others 1960a) while bargad leaves (*F. bengalensis*) did not provide sufficient nutrients to maintain bullocks (Mia and others 1960b).

Digestion values for leaves collected in 1970 from two evergreen and two deciduous woody species are found in fig. 3. Evergreen yaupon (*Ilex vomitoria*) leaves were about 75-percent digestible throughout the year while semievergreen leaves from coppice growth of willow oak (*Quercus phellos*) were poorly digested at all seasons. Anatomical characteristics such as thickened cuticles and cell walls, high fiber content, and the presence of significant amounts of waxes, resins, and tannins lessen the food value of

Table 3.--*Nutrient content (Means ± SE) of the terminal 4 inches of current twigs and leaves of American beautyberry*[1]

Fraction	Current Twigs[2]	Leaves[3]
	Percent[4]	
Dry matter	54.1(2.0)	35.2(1.4)
Crude protein	5.9(0.3)	14.8(0.9)
Crude fat	1.9(0.2)	7.8(1.0)
Ash	4.7(0.2)	8.9(0.3)
Crude fiber	43.6(1.0)	15.1(0.5)
Nitrogen-free extract	43.9(0.7)	53.4(1.1)
Cell wall content	70.5(0.8)	31.5(1.7)
Cell content	29.5(0.8)	68.5(1.7)
Acid detergent fiber	53.7(0.5)	24.3(1.6)
Acid detergent lignin	14.5(0.4)	7.1(0.3)
Cellulose	34.7(1.0)	18.5(0.9)

[1]Data from Short and Harrell 1969.
[2]Values for 12 monthly collections.
[3]Values for seven monthly collections.
[4]Values other than those for dry matter are percentages of ovendry weight.

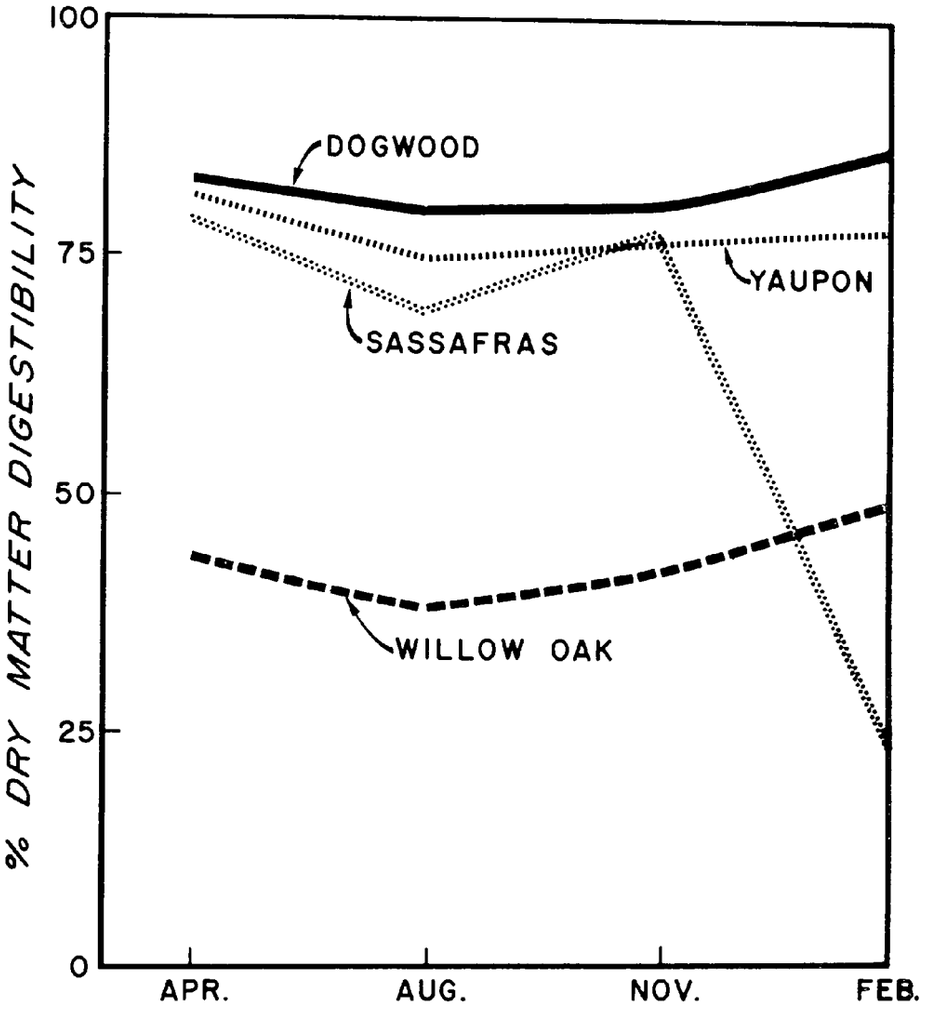

Figure 3.--Digestibility of leaves of four woody species at the four seasons.

oak leaves (Mackie 1903). Digestion of dogwood (*Cornus florida*) and sassafras leaves were similar in April and November but somewhat divergent during August. Dried and fallen dogwood leaves collected in late January were as digestible as the living tissue (about 85 percent), while dead sassafras leaves were only 25-percent digestible. These data suggest that the relative decay rates of the leaves from the two woody species may differ. In general, the digestibility of fallen leaves should be expected to diminish because of the translocation of soluble nutrients into proximal twigs before abscission and the leaching of nutrients from leaf tissues after abscission. Dead leaves gathered in the winter from several species of trees in east Texas contained little protein, intermediate levels of fiber, and high levels of lignin; they were of low *in vitro* digestibility (Short 1969).

Leaves vary in nutrient quality (Blair and Epps 1969) and digestibility throughout the year. Environmental factors that affect photosynthetic activity also modify the nutrient content and digestibility of leaf tissues. Sometimes suppressed trees have higher nutrient levels in foliage than do dominant trees (White and Carter 1968). Our data show that sassafras leaves from an unburned site were significantly less digestible than those leaves collected from a recently burned area (table 1). Position of leaf on the twig did not affect leaf digestibility from either site.

Physical and chemical properties

Spines, barbs, and hair may reduce the digestibility of shrub tissues by herbivores. A variety of glycosides, alkaloids, other toxins, and abnormal mineral constituents sometimes cause animal illness or death (Mueggler 1970). Constituents affecting shrub palatability and the role of animal behavior in selecting foodstuffs are not well

understood. Fertilization of woody species may increase animal preference, microbial rumen fermentation rates, and nutrient quality of shoot growth (Oh and others 1970). The proximity of browse plants to legumes seems to increase their selectivity by deer (Davidson 1970).

Antimicrobial substances, such as essential oils, sometimes affect rumen fermentation capabilities or the palatability of plant tissues. Northern white-tailed deer (*Odocoileus virginianus*) eat white cedar (*Thuja occidentalis*) extensively during the winter, even though cedar browse has fungicidal, bacteriocidal, and bacteriostatic properties. The rumen microbes of experimental deer were not as affected by the antimicrobial substances in white cedar as were the rumen microbes of an experimental steer also fed white cedar (Short 1963). Oils from Douglas-fir (*Pseudotsuga menziesii*) needles contain over 25 different compounds, 20 percent (by volume) of which are oxygenated monoterpenes that inhibit rumen microbial activity (Oh and others 1967). Different genotypes of Douglas-fir and different woody species vary in oxygenated monoterpene concentrations and in their inhibitory effects on rumen micro-organisms (Oh and others 1968).

Nagy and Tengerdy (1968) have hypothesized that the absolute concentrations of volatile oils encountered in some sagebrush populations could potentially limit rumen microbial activity if these plants were the total food of mule deer. However, the potential inhibitory effects of antimicrobial components within shrubs are seldom realized in nature. Antimicrobial substances act as repellents to limit consumption (Mueggler 1970) and antimicrobial substances may not be extensively liberated within the acid rumen. Kushner and Harvey (1962) demonstrated, for example, that the maximum rate of physical release of antimicrobial substances from leaves occurs at pH8-10. Another ameliorating factor is that at least some herbivores can excrete substances such as the essential oils (Cook and others 1952). Thus, shrubs high in essential oils have high gross energy values but relatively low metabolizable energy levels.

Antimicrobial substances in leaves can affect consumers through other pathways than animal selection or ruminal disfunction. The presence of tannins in oak leaves can form complexes with leaf protein so that the digestibility of leaf protein by phytophagous insects is reduced. Leaf protein in these cases is readily digestible only during early leaf development or by those insects which have high gut pH values (Feeny 1969).

Conclusions

Phenological changes in twig tissues affect the digestibility of woody shrubs throughout the year because newly formed tissues are more digestible than mature tissues. Genetic, metabolic, and environmental factors influence nutrient content and cell wall structure of shrub tissues. When nutrient content is reduced or cell-wall components are increased, the apparent digestibility of shrub tissues declines.

Leaves and inner bark are generally more digestible than woody tissues. Exceptions occur when antimicrobial substances are present that influence animal selection or reduce digestive efficiency.

Physiological problems in animal use of shrubs as forage

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Mountains, valleys, foothills, and deserts in the arid shrub regions of the world produce millions of tons of vegetation. Chemical energy stored by plants is a source of useful potential energy for man. Plant materials supply feed, fuel, lumber, and chemicals; but the major part of this resource is converted to human use through grazing by livestock. Livestock use plant energy to produce high quality, desirable food and fiber for man (fig. 1).

The potential of plant materials as food for livestock must be evaluated if it is to be fully utilized. The first task in evaluation is to measure the inherent nutritive value of the plants. Two phases of this first approach were outlined years ago by Harris and others (1952). They include determination of the species composition and nutritive content of the animals' diets (Cook and others 1948; Cook and others 1951, 1952, 1954; Lancaster 1954; Torell 1954) and also the determination of specific influences on the chemical composition of a given plant species on the range (Cook and Harris 1950).

The second task is to devise measures that appraise the nutritional state of grazing animals. Body weight changes and the condition of the animal (visually evaluated) have been valuable indices of range utilization (Clanton and others 1959). More refined techniques to determine animals' condition with respect to specific nutrients are needed. These include use of the nitrogen-creatinine ratio to predict protein deficiency (Butcher and Harris 1957) and measurements of hypoproteinemia (low blood protein) (Stare and others 1958), blood phosphorus level, and level of vitamin A and carotene in the blood and liver (Guilbert and others 1937).

Determination of appropriate supplements to correct dietary deficiencies or toxicities revealed by the methods just outlined is the third task in achieving maximum use of plant materials for livestock, but it is outside the scope of this paper.

This paper reviews some basic methods of measuring nutritive value of shrubs and describes some attempts to solve nutritional problems of livestock in an arid shrub region.

Basic methods for determining nutritive value of shrubs

The basic methods outlined below were detailed by Harris and others (1967) and Harris (1970). The nutritional value of an animal's diet depends upon the amount and digestibility of each kind of feed consumed. Complete measured data are impossible to obtain. For animals grazing range or pasture, data must be estimated indirectly by

Figure 1.--Sheep grazing on winter desert shrub range in south-central utah. Vegetation is sparse. Note the playa in the background.

using both internal and external indicators. *Internal indicators* occur in the plant and provide an estimate of apparent digestibility; they include lignin, plant chromogens, nitrogen, the methoxyl group, and silica. *External indicators* are fed to animals to enable estimation of fecal output without using a feces bag. They include chromic oxide (chromium sesquioxide), iron oxide, and monastral blue.

Calculating forage intake and digestibility

Two techniques highly useful to the range nutritionist for calculating forage intake and digestibility by grazing animals are the *ratio technique* and the *fecal index technique*. Analysis of nutritive value of forage requires information about volume of dry matter consumed, apparent digestion coefficients (in percent) for both protein and dry matter, indigestible dry matter coefficient (in percent), dry matter consumption (DM), and fecal matter output (in grams). One or more of five equations shown below may be used to compute the necessary informational items listed above.

The following sample data and derived equations illustrate typical computations for sheep grazing on winter fat *(Eurotia lanata):*

Internal indicator fed: chromic oxide	10.0 g. per day
Winterfat, lignin, dry basis	13.0 percent
Winterfat, protein, dry basis	7.7 percent
Feces output (collected with bag or calculated by equation 5)	870.0 g. per day
Feces analysis (dry basis):	
Chromic oxide	1.15 percent
Lignin	22.6 percent
Protein	6.0 percent

The following equations may be used for computing or estimating dry matter consumed, apparent digestion coefficients for dry matter and protein, indigestible dry matter, dry matter consumption, and output of fecal dry matter.

Dry matter consumed

$$= \frac{\text{weight of internal indicator in fecal output}}{\text{\% indicator in forage}}$$

$$= \frac{870 \text{ g.} \times 22.6\% \text{ lignin in feces}}{13\% \text{ lignin in winterfat}}$$

$$= 1{,}512 \text{ g. dry matter consumed.} \qquad (1)$$

Apparent digestion coefficient (%), general

$$= \left[100 - 100 \times \frac{\text{\% internal indicator in forage}}{\text{\% internal indicator in feces}} \times \frac{\text{\% nutrient in feces}}{\text{\% nutrient in forage}}\right]$$

for protein

$$= 100 - \left[100 \times \frac{13.0}{22.6} \times \frac{6.0}{7.7}\right]$$

$$= 55.2\% \text{ apparent digestibility of protein} \qquad (2a)$$

for dry matter

$$= 100 - \left[100 \times \frac{13.0}{22.6} \times \frac{100}{100}\right]$$

$$= 42.5\% \text{ apparent digestibility of dry matter} \qquad (2b)$$

Indigestible dry matter (%)

$$= 100 - \text{\% digestibility of dry matter}$$

$$= 100 - 42.5$$

$$= 57.5\% \text{ apparent indigestible dry matter} \qquad (3)$$

Dry matter consumption (DM)

$$= \frac{\text{DM in feces (g.)} \times 100}{\text{\% indigestibility of DM}}$$

$$= \frac{870 \text{ g.} \times 100}{57.5}$$

$$= 1{,}512 \text{ g. dry matter consumed} \qquad (4)$$

Fecal dry matter output (g.)

$$= \frac{\text{external indicator fed (g. chromic oxide)} \times 100}{\text{\% external indicator in feces grab sample DM}}$$

$$= \frac{10 \times 100}{1.15}$$

$$= 870 \text{ g. fecal dry matter} \qquad (5)$$

The Ratio Technique

If the herbage ingested is properly sampled, and the internal indicator is completely indigestible, dry matter intake can be calculated as in equation (1).

The apparent digestion coefficient for each nutrient in the diet can be calculated according to the general equation (2). The ratio technique works well only when an accurate sample of the forage consumed by the animal is obtained and the indicator is completely indigestible.

The most widely used internal indicators for the ratio technique are chromogen and lignin. Chromogen appears to be a good indicator for succulent green forage during the summer (Reid and others 1952); lignin is a good indicator for winter range plants (Cook and Harris 1951).

Fecal Index Technique

To obtain data for this method, forage is clipped and fed during a conventional digestion trial using a digestion stall; the quantities of forage intake and the fecal output of a few animals are measured. The feed and feces are then analyzed for an internal indicator, and for gross energy, organic matter, nitrogen, silica-free dry matter, or other dry matter. The internal indicator need not be indigestible, but that would be ideal. Correction is made for digestibility by using a regression equation (fig. 2).

During a conventional digestion trial, animals either equipped with fecal bags or fed an external indicator are grazed on the pasture, and the concentration of the internal indicator in their feces is determined. Regression equations for the data on the animals fed in the conventional digestion trial are then calculated and used to determine the digestibility of the forage.

When a regression equation has been obtained for a particular set of pasture conditions, digestibility can subsequently be calculated from the concentration of the internal indicator in the feces. It is essential to note, however, that a regression equation determined for one set of conditions does not work under all sets of conditions. Each research worker should therefore determine his own regression equation or make sure that someone else's equation applies to his own experimental conditions. The regression formula for the line will not always be linear, but the steeper the slope the more reliable the estimate.

By using the relevant data, the dry matter intake can be calculated (equation 3) as the complement of the percent indigestibility of the dry matter, and the dry matter consumption can then be computed by equation (4).

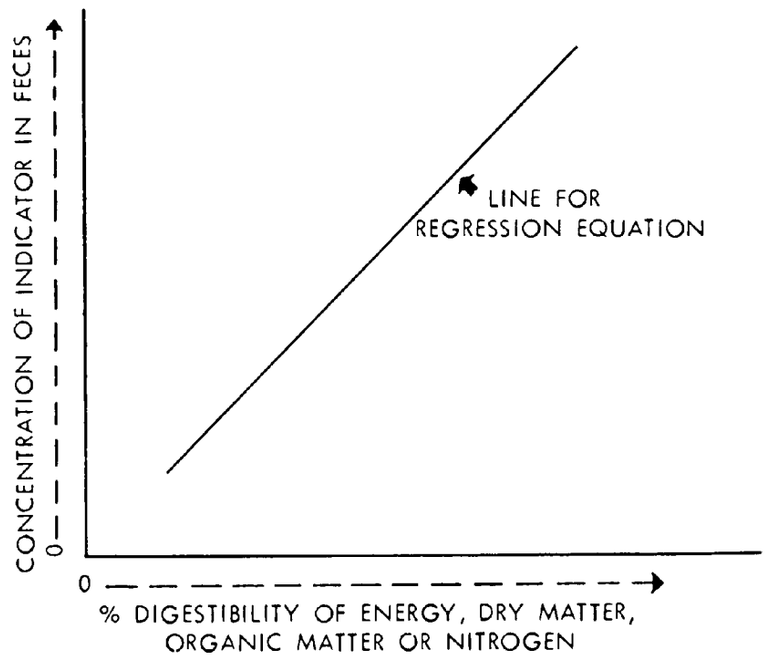


Figure 2.--Schematic of regression equation to predict digestibility from concentration of internal indicator in feces.

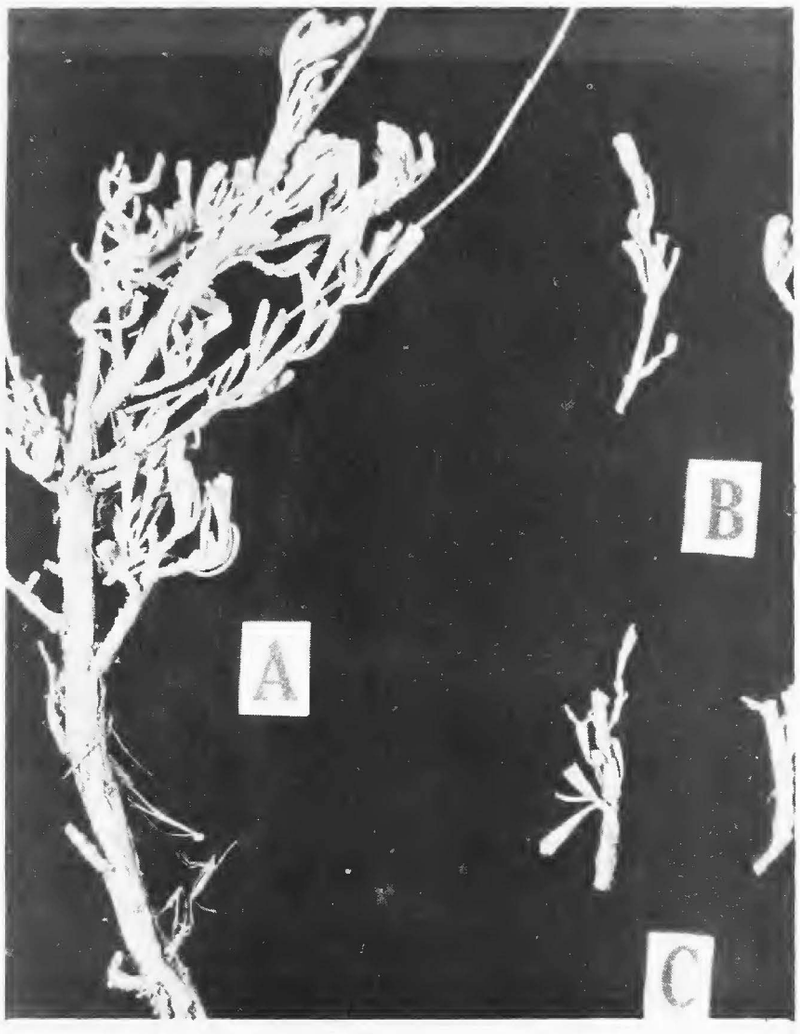


*Figure 3.--An observation (A) containing many units is collected for browse species such as big sagebrush (*Artemisia tridentata*). Before-grazing units (B) and after-grazing units (C) consisting of the current year's growth are picked off the observations.*

Estimation of Total Feces by Grab Samples

If a collection bag cannot be used, a grazing animal can be fed a measured amount of an external indicator, and small grab samples of feces may later be removed manually from the rectum or collected at random from the pasture at various times during the day. Calculating the total output of fecal dry matter is done by using equation (5). At least 50 grab samples should be taken from each animal to keep the error below 5 percent, and the indicator should be fed for at least 10 days before the start of sampling.

Obtaining samples of forage ingested

Under winter range conditions in arid regions, a sheep's diet is composed of a few shrub species and fewer grasses. In winter these plants are cured on the stem and are relatively high in lignin but low in chromogen. With mixed species of this type, it is impossible to hand-collect forage samples that represent the animals diet in the field. To obtain the data necessary for the forage nutrient analyses, we have used the "before and after" method plus the lignin ratio technique to compute the dry matter intake and its digestibility.

The "Before and After" Method

By this method the dry weight and chemical composition of the available forage of each species on a pasture are determined before and after grazing (Cook and others 1948). The amount of available forage is measured by collecting, along transect lines, plant units from each species before and after grazing (fig. 3). The difference represents the animal's diet.

Table 1.--*Method of calculating botanical and chemical composition of a sheep's diet on a winter range*

Species and sample	Average density[1] per 100 sq.m. (1)	Units per sq.m. (2)	Average wt per unit (3)	Wt.per sq.m. density (col.2X3) (4)	Total wt.per 100 sq.m. (col.4X1) (5)	Amount consumed (6)	Utilization (7)	Diet (8)	Protein content (col.9X5) (9)	(10)	Crude fiber content (col.11X5) (11)	(12)	Calcium content (col.13X5) (13)	(14)	Phosphorus content (col.15X5) (15)	(16)
			- - - - - *grams* - - - - - - -			*g/100m²*	%	%	%	*g/100m²*	%	*g/100m²*	%	*g/100m²*	%	*g/100m²*
Atriplex confertifolia																
Before grazing	1.3	4,370	0.1231	538	699				6.88	48	33.3	233	2.59	18	0.069	4.8
After grazing	1.3	4,370	.0921	402	523				6.50	34	35.9	188	2.19	11	.062	3.2
Diff. (ingested)						176	25.2	4.93		14		45		7		1.6
Eurotia lanata																
Before grazing	3.2	2,282	.5264	1,201	3,843				10.12	389	36.7	1,410	1.50	43	.099	3.8
After grazing	3.2	2,282	.3321	758	2,426				9.00	218	39.0	946	1.37	33	.095	2.3
Diff. (ingested)						1,417	36.9	39.66		171		464		10		1.5
Gutierrezia sarothrae																
Before grazing	2.4	6,480	.0946	613	1,471				6.62	97	24.0	353	1.13	17	.079	1.2
After grazing	2.4	6,480	.0854	553	1,327				6.53	87	24.8	329	1.13	15	.076	1.0
Diff. (ingested)						144	9.8	4.03		10		24		2		0.2
Sporobolus cryptandrus																
Before grazing	1.7	180	3.443	6,197	10,535				4.13	535	39.9	4,203	.48	51	.069	7.3
After grazing	1.7	180	2.843	5,117	8,699				4.02	350	43.5	3,784	.40	34	.065	5.7
Diff. (ingested)						1,837	17.4	51.38		185		419		17		1.6
Total (ingested)						3,573				380		952		36		4.9
Percent in diet								100.00	7.85		26.80		1.36		.096	

[1]Represents normal ground cover of each species without artificial rearrangement of the foliage to arrive at the percent density.

The unit collected for most browse plants consists of twigs of the current year's growth: for bunchgrasses, the entire clump; for semibunchgrasses, only the individual stem; for sod grasses, measurements either on a 1/16-square-foot of sod or of individual tiller stems; for annuals and most forbs, either the aerial parts of the plant or an individual stem; and for some coarse broadleaved forbs, the leaf and leaf stem. Forage samples collected by this system are not contaminated by saliva; therefore, mineral analyses can be made.

Table 1 illustrates the method of calculating the botanical and chemical composition of the sheep's diet based on this method. Total intake of forage and the digestibility of its protein and crude fiber can be obtained by the lignin ratio method (equation 1). This "before and after" method is especially valuable on an arid winter range. In winter the plants are relatively dormant and corrections do not need to be made for growth between collections. Plants (predominantly shrubs) are far enough apart that shattering and trampling are not problems.

Esophageal Fistula Method

A representative sample of a grazing animal's diet is best obtained from the foraging animal itself. Animal-gathered samples were first collected in California by using an esophageal fistula (Torell 1954). The fistula in the esophagus of the sheep was closed by pulling the wool over the opening. We modified this technique by inserting a plastic cannula with a cap into the esophagus (Cook and others 1958). Improved operative techniques and a removable cannula (fig. 4) were outlined by Harris and others (1967) and by Harris (1970). Animals are fitted with plastic bags to collect a sample of the sheep's diet (fig. 5).

The esophageal fistula provides accurate samples of a sheep's diet under most conditions. If a sample is used for chemical analysis, however, certain corrections need to be made for contamination by saliva (Bath and others 1956; Van Dyne and Torell 1964). There seems to be little contamination of protein, but considerable contamination of minerals. Intake and digestibility are calculated by the ratio technique using equations (1) and (2).

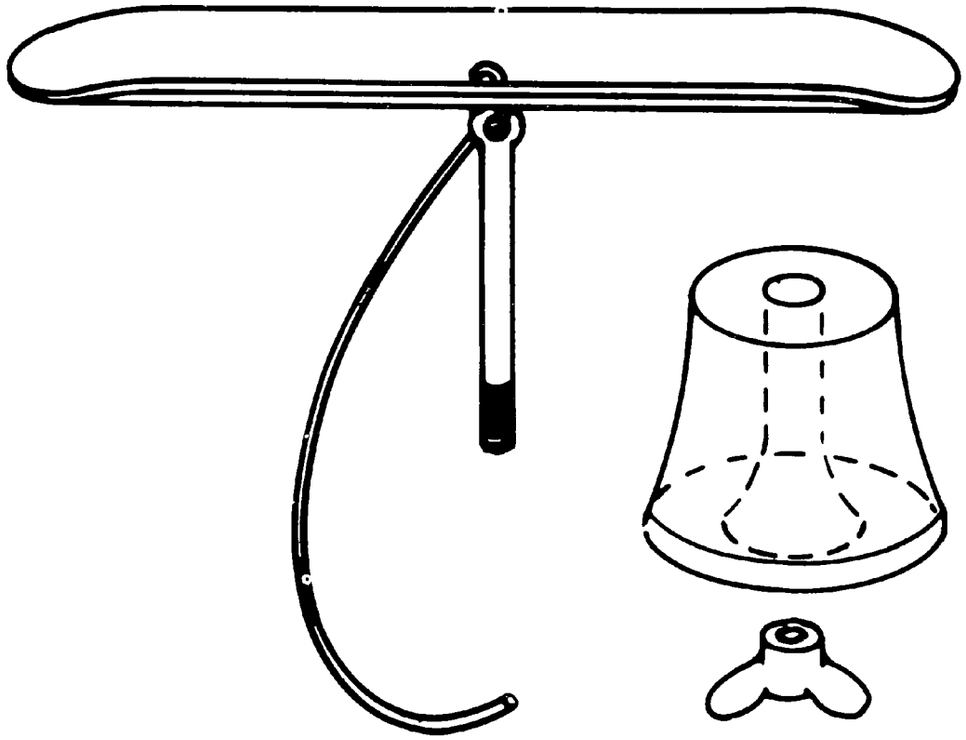


Figure 4.--An improved esophageal cannula. (Available from Precision Machine Company, 2933 North 36 Street, Lincoln, Nebraska.)

Figure 5.--This sheep is equipped with an esophageal fistula and cannula. As the sheep eats, the diet is sampled and falls into the bag. When the animal is not sampling forage, the fistula is closed by a plastic cap on the cannula.

Rumen Evacuation Method

To sample the grazing animal's diet by the rumen evacuation technique, a cannula is inserted into the rumen (Harris 1970). For diet sample collection the contents of the rumen and reticulum are first completely removed (Lesperance and others 1960). Then it is advisable to quickly rinse the rumen and remove the water with a small pump before sampling. The animals are then allowed to graze for 0.5 to 2 hours depending on availability of forage. The forage sample is then removed from the rumen and reticulum and the original contents are put back in. Diet samples collected by this method are contaminated with saliva, and corrections are needed as described for the esophageal samples. This method gives a total collection and is better than the esophageal fistula method for sampling some coarse dry grasses.

Measuring metabolizable energy of range plants

The total digestible nutrient (TDN) content of big sagebrush, black sage, and similar browse plants was determined and found to be exceptionally high in TDN compared to their value when fed to the animal. Therefore, methods were devised to measure the metabolizable energy (ME) of range plants (Cook and others 1952), defined as:

ME = gross energy intake - (feces energy, urine energy, and methane energy).
Wethers equipped with fecal bags and urinals were kept in temporary enclosures (fig. 6). Methane was calculated by using Swift's (1948) formula:

$$\text{methane (g.)} = 2.41 \times 100 + 9.8$$ (X represents grams of ingested digestible carbohydrates + crude fiber + nitrogen-free extract)

Each gram of methane has a caloric value of 13.34 kilocalories. Blaxter (1962) suggested that methane may be calculated from the gross energy consumed.

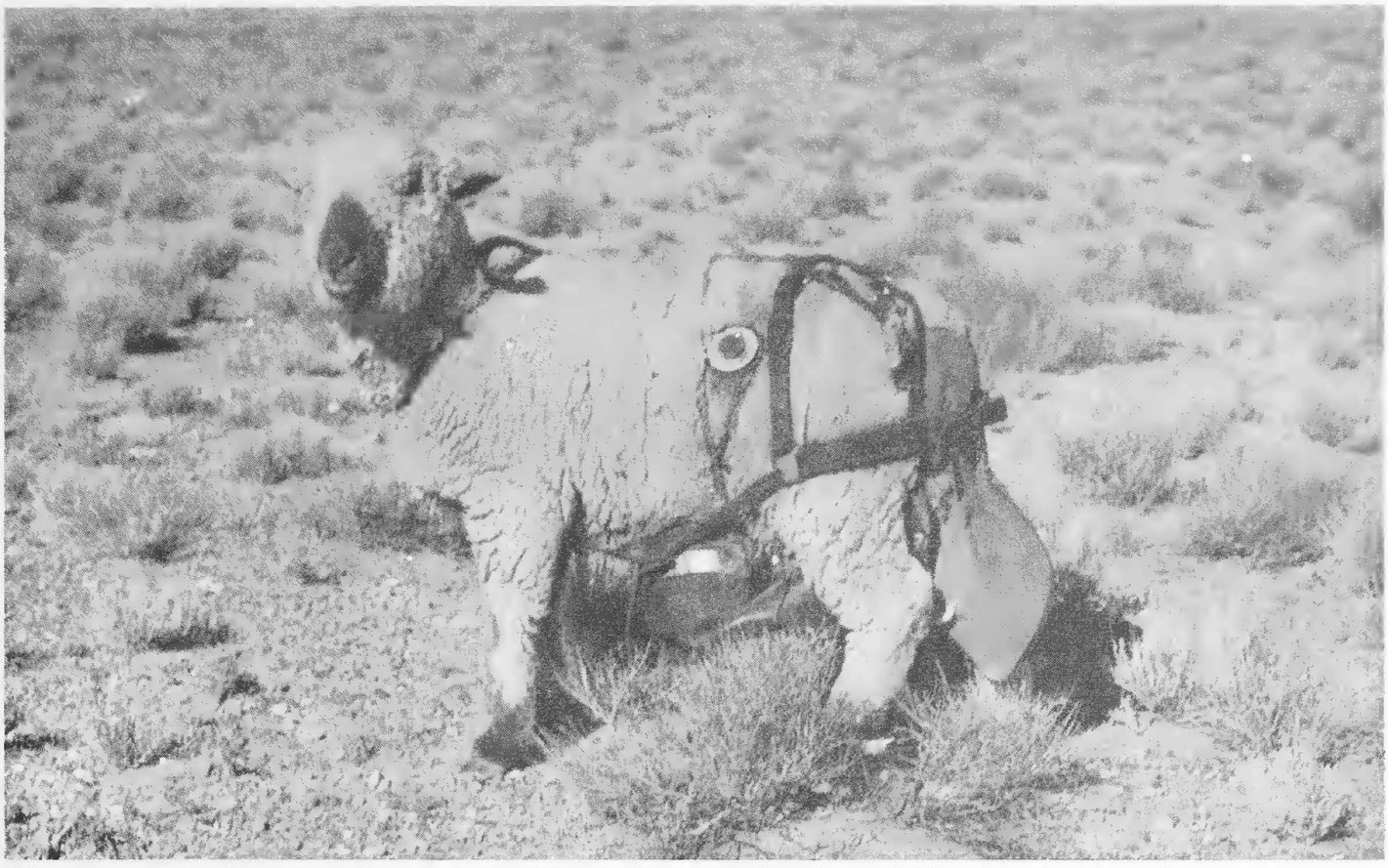


Figure 6.--A sheep equipped to collect feces and urine while grazing on the range so that the energy of the feces and urine may be determined. The sheep also has a rumen fistula for introducing supplements into the rumen.

The following tabulation of comparative energy values for three important desert range shrubs shows that black sage (*Artemisia nova*) and big sagebrush (*A. tridentata*) are high in gross energy (GE), digestible energy (DE), and TDN, but much lower than squirreltail grass (*Sitanion hystrix*) in metabolizable energy (ME). (GE, DE, and ME are given in kilocalories per kilogram, TDN in percent.)

Species	*GE*	*DE*	*ME*	*TDN*
Black sage	5,101	2,124	1,044	49.5
Big sagebrush	4,830	1,948	1,130	43.4
Squirreltail grass	3,787	2,022	1,704	50.4

The characteristic differences between squirreltail grass and the other two shrubs may result from the rather large content of volatile oils in black sage and big sagebrush; therefore metabolizable energy appears to be a better index of energy value of some range plants than either digestible energy or TDN.

Expressing energy values

The nutritional requirements of animals and the energy value of feeds and diets have been expressed in the United States primarily in the TDN system. However, in 1955 the Animal Nutrition Committee of the National Research Council (NRC) passed a resolution to express energy requirement in calories and requested that information be gathered on the GE, DE, ME, and net energy (NE) of feeds and diets so that the TDN system could be replaced. The calorie system (fig. 7) is now being used in all the NRC Nutrient Requirement Reports and by the NRC Animal Nutrition Committee on Feed Composition (Crampton and Harris 1964).

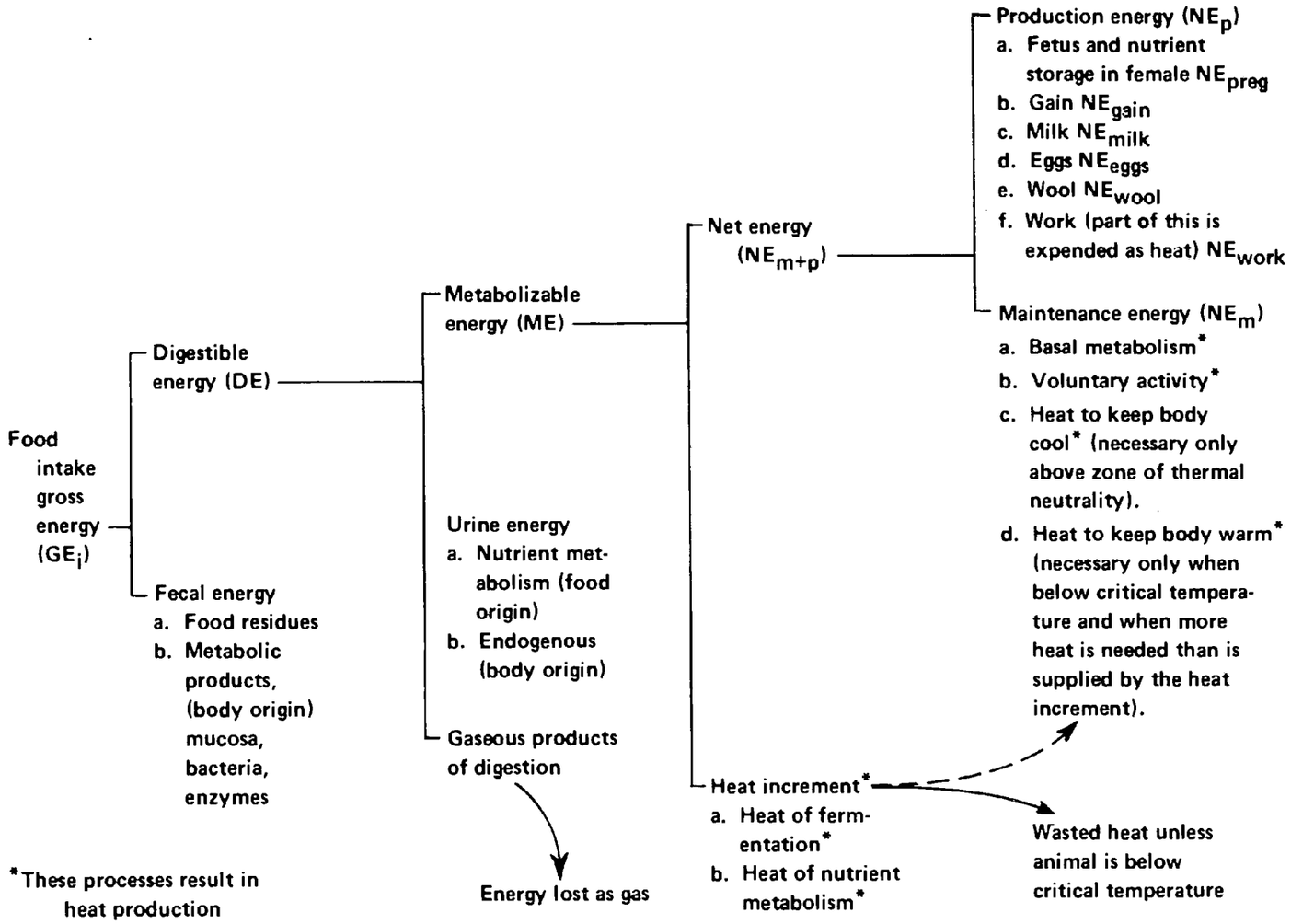


Figure 7.--The conventional scheme of partition of food energy as it is utilized by the animal.

The Animal Nutrition Committee of the National Research Council in November 1958 adopted 4.409 kilocalories per gram (2,000 kilocalories per pound) of TDN to convert it to DE (Crampton and others 1957; Swift 1957). The formulas now being used by the NRC Animal Nutrition Committee on Feed Composition (Harris and others 1968; Crampton and Harris 1971) include:

$$\text{DE (kcal./kg.)} = \frac{\text{TDN \%}}{100} \times 4{,}409$$

$$\text{ME (kcal./kg.) for ruminants} = \text{DE (kcal./kg.)} \times 0.82$$

$$\text{ME (kcal./kg.) for swine} = \text{DE (kcal./kg.)} \frac{96 - (0.202 \times \text{protein \%})}{100}.$$

Net energy values for some cattle feeds including net energy for maintenance (NE_m) and net energy for gain (NE_{gain}) may be estimated from a formula developed by Lofgreen and Garrett (1968):

$$\text{Log } F = 2.2577 - 0.2213 \text{ ME}$$

$$NE_m = 77/F$$

$$NE_{gain} = 2.54 - 0.0314 F.$$

The terms used in these formulas were defined by Harris (1966) on a dry-matter (moisture-free) basis.

1. F is the grams of dry matter per unit of $W^{0.75}$ required to maintain energy equilibrium.

2. ME is the metabolizable energy in kcal./g. of dry matter (DM) (or megcal./kg. DM).

3. NE_m is the net energy for maintenance in kcal./g.DM (Mcal./kg.DM),

4. NE_{gain} is the net energy for gain in weight in kcal./g.DM (Mcal./kg.DM).

To convert NE_m and NE_{gain} to kcal./kg. the values are multiplied by 1,000.

Some of the formulas were developed under farm conditions rather than range conditions; however, they may be used until more adequate ones are devised.

Measuring distances traveled by grazing sheep and cattle

Cattle and sheep travel long distances to obtain feed and water when grazing rangeland. Since they expend considerable energy, the distance they travel is relevant when calculating energy requirements.

Our first studies included use of a range meter that was developed for measuring the distance traveled by sheep (Cresswell and Harris 1959). In a pasture of 259 hectares (1 mile square) on a winter saltbush-type range, sheep averaged 4.6 km. (1.6 miles) a day to obtain their feed (Morris and others 1965).

Experiment on a winter shrub range

An experiment conducted in Pine and Wah Wah Valleys in west-central Utah on a shadscale range (Harris and others 1956) illustrates development and application of several classic techniques (Harris and others 1952) to solve problems on a winter range. This experiment was designed to calculate the nutrient content of a grazing sheep's diet. The percentage composition of the diet of our experimental sheep was determined by the "before and after" method. Digestibility and intake of dry matter were determined by the lignin ratio technique. Metabolizable energy was determined by collecting and analyzing the feces and urine for energy and estimating the energy in the methane as described previously.

When the nutrient content of the diet of these experimental sheep was compared with the nutritive requirements of a 130-pound ewe as proposed by the National Research Council (1949), the diet was low in phosphorus, protein, and energy but was exceedingly high in calcium.

The future

As the questions we ask through research become more exacting, the techniques at our disposal must become more accurate and reliable. Hence, part of our work is necessarily concerned with development of better techniques. From experience reported above, certain research needs are directly apparent; a few examples are:

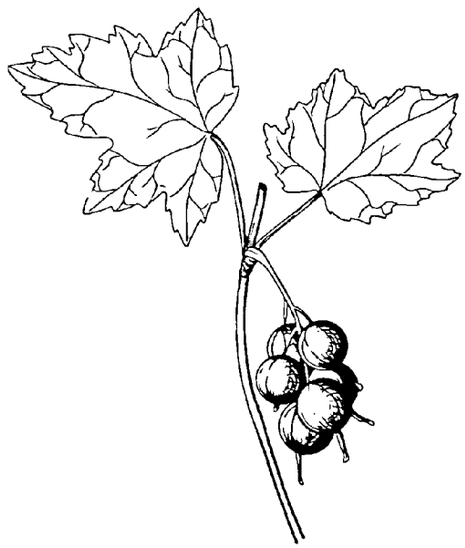
1. Methods to measure directly the nutritional condition of an animal.

2. A simple indicator for estimating urine output similar to the system for estimating feces output by using chromic oxide.

3. A satisfactory internal indicator for use in digestibility studies.

4. A method for collecting diet samples without contamination by saliva. This list could be augmented considerably, but it is suggestive.

If we expect an expanding population to continue eating beefsteak and lamb and drinking milk, we must find a more efficient way for ruminants to utilize poor range forage and cornstalks; otherwise, such protein feeds as soybean meal will have to substitute for meat, poultry, and milk. An improvement in the efficiency with which vegetation can be converted to food and fiber will obviously be valuable to society economically and sociologically. An arid region is not necessarily unproductive, but it presents greater challenge to human ingenuity. Nutritional scientists are accepting that challenge.



Goat response to use of shrubs as forage

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The world's goat population of 375 million head has increased about 30 percent within the last 20 years. The widespread and increasing use of goats is mainly the result of the following: (1) Today's deteriorated ranges furnish forage more suitable for goats than for other kinds of livestock; (2) goats provide meat, milk, and mohair at relatively low levels of management and investment; and (3) goats have attributes that favor their use over other kinds of livestock. In respect to this last, the goat is a small animal that requires a relatively short time to mature and so requires less feed between birth and production. Furthermore, its potential for milk and meat production is considerable under proper care. The goat requires little space and due to its versatility can be raised on almost any kind of feed, although not all feed is conducive to maximum production.

Worldwide goat production could be considerably increased through improved pasturage or nutrition particularly in shrublands. Since research on nutritional requirements of goats is very limited, this paper is necessarily an indirect rather than a direct approach to goat response to use of shrubs as forage with the exception of research currently in progress in Mexico.

The goat controversy

Two conflicting views prevail as to the role of goats in land use: (1) The goat is the major cause of deforestation, rangeland destruction, and soil erosion; and (2) this animal is of considerable value and can be included in a rational grazing program. It is difficult to say when the goat controversy began, but the earliest references found were those by Hall (1936) and Hornby (1936). As a Heath Clark Lecturer at the University of London in 1935, Hall said:

> The greatest danger, however, lies in the fact that overgrazing may so destroy the vegetation and bare the surface that soil erosion sets in....of all livestock the goats are the worst offenders....The brunt of the campaign against overstocking should fall on the goats....

At about the same time, Hornby wrote:

> The goat is often referred to as though its depredations exceeded those of other animals. The reason for this is that this species is more injurious to trees than are cattle and sheep, and that it bears the double blame of destroying both forests and land. This is not quite fair. The cattle and sheep have created a wilderness

> of gullies separated by dry ridges bearing nothing in the way of vegetation but the hardiest of shrubs, the cattle and sheep have departed with the last of the grass, the goat still to be found and as he valiantly extracts a livelihood where no other animal can live, he undoubtedly makes yet steeper the sides of gullies, and appears to be doing his best to remove the last of the plants and with them the last of the soil. But, in reality, he is merely completing the destruction wrought by sheep, cattle, donkeys and man.

These differences of opinion have caused varying governmental approaches pertaining to goats. Venezuela has stopped its *"Campañas de Erradicación de Chivo,"* campaigns for the eradication of goats (Hernández 1971). Other examples, taken from the *Report of the Meeting of Experts Organized by FAO and FAAP on Production and Utilization of Sheep and Goat Milk in the Mediterranean Region* (FAO 1961) note that: goat numbers have dropped in Yugoslavia because of enforcement of laws to increase sheep husbandry; goat numbers have increased in Italy because of removal of the governmental tax on goats; France does not consider goats to be a problem; a recent policy in the Egyptian region of the UAR discourages goat breeding; goats have always been recognized as valuable milk and meat producers in the Syrian region of the UAR and the excellent Damascus goat is being improved by private breeders; Swiss farmers are reducing goat numbers; many Portuguese municipalities have laws banning goats and other laws protect forests from goats as well; Cyprus depends heavily upon goats for cheese manufacture and has a large program to increase goat production under way; Israel, which favors keeping improved goats in stalls, has laws that have eliminated goat flocks to a large extent. The experts concluded the meeting by recommending that FAO carry out a comprehensive inquiry on the legislative measures regulating goat breeding in the various Mediterranean countries, "in the hope that uncontrolled and low-producing goat herds of these countries will be replaced by selected profitable herds kept under stabled or tethered conditions.

To categorically blame the goat for the vast destruction of the world's pasture and forest resources is unrealistic. The best approach would be to develop a thorough understanding of the goat and to place it in a rational grazing program. The problem is not the goat *per se,* but uncontrolled and continued overgrazing (FAO 1969; Harvey and Rigg 1964; Agraz 1970; Devendra and Burns 1970; FAO 1966; and Le Houérou 1964). Man is the true culprit in the destruction of vegetation by domestic livestock. However, concern over continued overgrazing by goats is justified. In some areas, the appropriate question may be "what other kind of livestock do we have to graze these lands when goat pasturage is destroyed?"

Most of the world's deteriorated rangelands were caused by being overgrazed by cattle and sheep. Eventually, overgrazing left pasturage only the goat could utilize--in many cases, browse or shrubs. This is not to say that all shrublands are a result of overgrazing, but that goats are now producing in many areas where other kinds of livestock can no longer produce. Thus, the world's goat production is largely due to this animal's use of shrubs as forage. However, a highly important question remains, "Is this the best use of the land?"

The goat's diet

All animals feed selectively, and the goat is no exception. However, Le Houérou (1964) stated that goats are less selective than sheep. Wilson (1969) concluded from his review of the literature that goats eat more browse than sheep which in turn eat more than cattle. In the Mediterranean area, goats eat both brush and herbaceous species, but show a marked preference for brush (FAO 1953). Edwards (1948) observed

that goats never grazed grasses during shrub leaf flush and Carrera (1969) reported that goats ate browse almost exclusively in the arid zones of Mexico.

Observations of 1,728 goat bites in a mixed brush-grass-forb community in Mexico revealed that 83 percent of the bites were on browse and forbs and 17 percent on grass (Carrera 1971). Farps and Cory (1940) stated that browse constituted more than 50 percent of the goat's diet from July to August and November to January in the Edwards Plateau of Texas. They also observed that goats utilized a wide variety of species and, at times, heavily consumed forbs and grasses.

McMahan (1964) observed one goat's grazing behavior in pastures that had histories of heavy, moderate, light, or no grazing use. He observed that browse constituted more than 50 percent of the annual diet regardless of past grazing use or forage availability.

Palazón (1953) stated that goats in Spain ate brush in the dry season and grasses, legumes, and forbs in the wet season. French 1970) reported diverse plant species and forage types in the goat's diet. Huss (1954) observed that goats grazed both brush and herbaceous species following the burning of the Juniper Woodlands in Texas. Goats selected species of *Quercus* and *Rhus* and would graze other woody plants only in overgrazed areas. They relished the pods of mescal bean *(Sophora secundiflora)*, ejecting the seeds from their mouths. The mescal bean was disseminated in this manner as are the fruits of *Gordia boissieri* in Mexico.

Huss and others (1970) and Zertuche (1970) observed in a study near Montemorelos, N. L., Mexico, that goats preferred browse even when exposed to an abundance of grass. Degree of grass, forb, and browse utilization on stocked pastures (7 and 14 goats per 5 hectares) was estimated throughout the year as being "slight," "light," "moderate," "heavy," or "severe." Grass utilization in all treatments was always "slight," except near fences and corrals where utilization ranged from "moderate to heavy." No evidence was found to indicate that the goats had consumed large quantities of forbs, but certain brush species clearly had been preferred to the exclusion of others. Thus, the selectivity of goats as to kinds of forage as well as species within the shrub classification was clearly demonstrated.

By means of esophageal fistulae, Malechek (1970) found that goats' preferences under both light and heavy grazing were seasonal, depending upon forage availability and stage of growth. Goats showed distinct preferences for grass from June to October even though browse was available. Browse was an important food item, especially in winter and early spring. The botanical composition of browse was different between the two stocking rates. Composition differences were partially due to range condition in addition to stocking rate. Browse was eaten during all seasons of the year and averaged 38.9 percent in the annual diet of goats in the lightly grazed pasture and 37.6 percent in the heavily grazed pasture.

A committee of experts concluded after evaluating grazing studies in Texas at the Ranch Experiment Station, Sonora, and the Kerr Wildlife Management Area, Hunt, that browse had been utilized more heavily in all pastures where goats were present (Anonymous 1957). They also determined that six Angora goats were equivalent to one cow or five sheep in respect to their effect upon vegetation and quantity of forage consumed.

The literature indicates that goats tend to eat more browse than grasses and forbs. Why the goat eats browse when other domestic livestock will not is a subject that warrants more research. This tendency may be due to nutritional demands. Gray (1959) stated that Angora goats can be grazed on grassland, but that mohair production will be less than on shrubland. Huston and Shelton (1967b) found that live oak (*Quercus virginiana*) leaves fed as a supplement to a balanced ration increased mohair production. Maher (1945) believed that goat's ability to consume browse is due to its mouth; a mobile upper lip and a very prehensible tongue permit the goat to eat short grass and

browse not normally eaten by other domestic livestock. This characteristic, which has been personally observed, enables goats to feed on browse in areas that offer no other choice.

In summary, it appears that the goat can cope with a variety of dietary alternatives. This flexibility explains its wide ecological distribution and extreme value in areas of adverse forage conditions, particularly shrublands. However, it is reasonable to assume that an ideal goat diet would not consist solely of browse, but that browse would be included and perhaps would be the major portion of feed consumed.

Nutritional considerations

Devendra and Burns' summary (1970) of goats' nutritional requirements did not reveal anything exceptional. However, there was some evidence that the goat might have an exceptional ability to digest crude fiber and that nutritional requirements may vary between breeds. Brody (1945) and Gaines (1943) have shown that the gross energetic efficiency of milk production in dairy goats is of the order as that of dairy cattle. However, maintenance requirements are double those of cattle (Gaines 1943). Research at the Texas A&M University Agricultural Experiment Station, McGregor, Texas, and local producer experience indicate that protein requirements of Angora goats are higher than those of other livestock. This high protein requirement may be a critical factor in the Angora's ability to survive periods of stress (Huston and Shelton 1967a). A study indicated that a protein level of up to 20 percent would be desirable for billy kids. Death of kids in Mexico is high, probably because of inadequate protein.

Malechek (1970) used esophageal fistulae to compare goat diets under heavily and lightly grazed conditions on the Texas A&M University Agricultural Research Station, Sonora, Texas. He found that differences in production could only partially be explained by differences in the quality of forage consumed because differences for a particular dietary nutrient were usually not large. He concluded that production was mainly due to greater forage intake during the spring in the lightly grazed pasture where there was greater forage availability.

The difference in goat response in Malechek's (1970) study could have been due to something that he could not detect in his analyses. March and April diets in the lightly grazed pasture consisted mainly of forbs and immature leaves of shin oak (*Quercus pungens* var. *vaseyana*), whereas in the heavily grazed pasture diets consisted mainly of pricklypear (*Opuntia lindheimeri*) juniper (*Juniperus* spp.), and some shin oak. Huston and Shelton (1967b) found that protein retention was increased when leaves of liveoak (*Quercus virginiana*) were included as an additional ingredient in the ration. Something in oak leaves may improve utilization of digested protein.

Carrera (1969) stated that 20 browse species constituted goat feed on a Northern Mexico range, and although protein content varied from 5.7 to 26.5 percent between species, there was little variation within species during the year. Supposedly, the goats had access to adequate protein throughout the year, yet, animal production was variable. He believed this was due to low energy consumption. Singh (1968) reported that goats fed high and medium levels of T.D.N., irrespective of protein levels, produced more meat and milk than animals fed at low levels of T.D.N. and corresponding levels of protein.

Menzies (1967) stated that the period between weaning in the fall and good pasture conditions in the spring is critical to the kid's development in Texas; winter pasture conditions are inadequate to sustain growth. Various dietary supplements increased body and fleece weight over the winter. Malechek's (1970) study also showed that the goat's winter diet was at its lowest nutritional level when it consisted mainly of browse and dry grass.

Huston and Shelton (1967a) suggested that poor nutrition is a much greater danger to animals that carry a high genetic potential for mohair production. This hypothesis is also supported by the poor performance of exotic and high potential breeds introduced into adverse nutritional conditions (FAO 1966 and Montsman 1967). These observations could explain some rather unexpected results of various studies conducted with "criollo" goats in northern Mexico. A daily feeding of 500 g. of ground sorghum 47 days before kidding significantly increased doe daily gains, but did not increase kid weights. Milk production increased during the first 59 days after birth, but the increase was not statistically significant (Carrera and Flores 1971). Phosphorus and cobalt supplementation did not increase milk production nor body weight in a grazing area supposedly deficient in both (Carrera and Mendizabal 1971). Flushing did not increase kid crop nor kid weight (Carrera and Diego 1971), and supplementation of grain sorghum and grain sorghum plus 4 percent urea only increased milk yields from 106 g. per day to 124 and 139, respectively (Carrera and Killian 1971).

Whether a goat requires more ash than other ruminants or whether his diet is high in ash because the animal eats large quantities of browse is unanswered. Malechek (1970) showed high ash consumption and Huston and Shelton (1967b) believed that mohair production was increased by a dietary supplement of live oak leaves because of their high mineral content.

Goat response as related to forage conditions

Various fundamentals of range or pasture management are too often forgotten in evaluations and investigations relative to the grazing of shrublands by goats. Too often, all shrub communities are considered to be excellent goat pasture, which is far from true. The world's low goat production level is in part due to inadequate forage even though shrub communities are bountiful. Shrublands have varying degrees of forage quality and quantity or forage conditions just as grasslands do. The forage condition of a specific shrub community depends upon the following: (1) Species composition; (2) acceptability of vegetative growth; and (3) accessibility of vegetative growth.

Species composition

Not all forage species are equal in palatability nor in nutritive value. Forage species are divided into three categories: desirable, less desirable, and undesirable. The fact that shrub species can be desirable, less desirable, or undesirable is often neglected in forage assessments of shrub communities--and this is especially true in the case of goats. As previously stated, goats are selective grazers and display preferences for certain shrub species.

An objective of range management is establishment of vegetation dominated by desirable forage species. Under severe nutritional stress, forced grazing of undesirable forage species will sustain a limited amount of animal life, but is not conducive to good production nor to good resource management. Such is the case in far too many goat grazing situations.

The number of desirable plant species in a particular plant community is primarily due to grazing. When one species within a community is eliminated for any reason, it is replaced by another or by an invading species (Oosting 1956). Continued overgrazing eliminates desirable forage species, which are replaced by less desirable or undesirable species. With continued destructive grazing, the less desirable species are eliminated and replaced by undesirable ones. This process can be reversed by management directed towards the establishment of desirable species.

Unfortunately, the goat's response to use of shrubs is poor in many situations simply because the community is dominated by undesirable species. Further, the situation is becoming worse in many cases because of continued overgrazing by goats.

Acceptability of vegetative growth

Acceptability of vegetative growth is related to species and tenderness of growth. Goats prefer leaves and tender twigs and do not consume tough woody growth (Malechek 1970); so a plant of a desirable species may be undesirable forage if a major portion of its growth is woody. On the other hand, the young tender growth of an undesirable species will definitely be more consumable if the goat has no other choice.

Manipulations that decrease the proportion of woody to herbaceous growth increase acceptability, as has been partially demonstrated by Huss and others (1970) and Zertuche (1970). Daily goat gains at the same stocking rates were significantly greater in pastures that were roller cut and burned after cutting than in pastures containing the original shrub vegetation (table 1).

Gains were attributed to the combined effects of acceptability and accessibility. Though it was impossible to separate the direct effects of each, increased acceptability was considered to be important. The young and tender sprouts that appear following roller cutting or burning after roller cutting were simply more palatable and perhaps more nutritious than the old and tough growth that dominated the original vegetation.

Accessibility of vegetative growth

Forage is defined as those plant species and plant parts that provide nutriments for grazing animals. Twigs and leaves beyond the animal's reach are not forage. Manipulations that increase accessibility will increase total forage production, as was partially demonstrated by Huss and others (1970) and Zertuche (1970). Roller cutting followed by burning increased accessibility by reducing average shrub height from more than 300 cm. to less than 72 (table 1). Percent shrub cover was significantly decreased by roller cutting followed by burning, yet, daily goat gains were less in the original vegetation of the pasture that had the highest brush cover mainly because the major portion of the growth was not accessible. Furthermore, percent forb cover and grass production per hectare were also increased by the two forage improvement treatments. Increased accessibility, acceptability, and, perhaps, forage quality were concluded to be the primary reasons for the increased daily goat gains, although grass probably played a secondary role.

Table 1.--*First-year effects of roller cutting and burning after roller cutting upon goat production and vegetation, Montemorelos, N. L., Mexico. Adapted from Huss and others 1970 and Zertuche 1970)*

Treatment	Shrub cover	Average shrub height	Forb cover	Grass production	Daily goat gains
	Percent	*Cm.*	*Percent*	*Kg./ha.*	*Grams*
Original vegetation	[1]86 A	300 A	12 A	452 A	191.7 A
Roller cut	62 B	72 B	20 B	1,146 B	252.8 B
Burned after roller cutting	37 C	64 B	24 B	1,628 C	250.2 B

[1] No statistically significant difference between same letters.

The degree of grass utilization was classified as slight in all pastures, but the quantity of grass ingested was probably different. Grass production improved from 452 kg./ha. in the control plots to 1,628 in plots burned after roller cutting (table 1). Slight use of 452 kg./ha. is considerably less forage consumed than slight use of 1,628 kg., which could have had an appreciable effect upon goat performance.

In summary, accessibility, acceptability, and species composition are important considerations to evaluations of forage conditions of shrub communities and to understanding goat response to use of shrubs as forage. A forage condition guide based upon these three factors could be developed for individual shrublands. Such guides would be conducive to a more rational use of these lands and to increased livestock production, especially goat production. Further research is needed relative to this concept, but more important is a general acceptance that shrublands *per se* do not necessarily represent excellent goat pasturage; many can be improved.

Goat response as related to dual use of shrublands

Goat grazing has increased mainly because overgrazing by other kinds of livestock has caused range conditions suitable only for goats. In such areas, goats provide income and food when other kinds of livestock could not. However, in many shrublands, complete dependency upon goats would result in a level of production somewhat below the potential. At times, goats would best fit into a dual grazing situation.

Dual use is the grazing of more than one livestock species on the same pasture at the same time or in rotation. The economic and productivity advantages of dual use have been demonstrated in the Edwards Plateau of Texas (Huss and Allen 1969; Merrill and Miller 1961). Several workers have obtained the same results in other parts of the world (Palazón 1953; FAO 1966). Merrill and Young (1954) reported a beneficial response in cattle and sheep grazed in combination with goats. However, no difference was noted in either the body weights or the mohair production of Angora goats dually grazed with cattle or with cattle and sheep. These data suggest that cattle and sheep respond more favorably than goats to dual use. However, Huss and others (1970) and Zertuche (1970) reported that practices which improve goat pasturage also improve pasturage for other kinds of livestock.

Both grass and goat production increased as shrub decreased (table 1). This and the fact that a stocking rate of 14 goats per 5 hectares was not detrimental to grass establishment suggests that dual use of goats and cattle is feasible without adverse effects to either. Dual use can result in greater total livestock production--and to the benefit rather than the expense of goats.

Interestingly, no significant difference in goat gains was associated with different shrub covers (37 and 62 percent) (table 1). If daily gain is a measure of total nutritive intake, then the 37 percent cover produced adequate feed for the stocking rates under trial and higher canopy cover offered no advantages. The foregoing suggests that optimum shrub cover exists for specific goat stocking rates. Such information will be valuable to estimates of stocking rates, particularly in dual grazing systems.

Goat response as related to management of shrublands

Goat production is influenced by overstocking. However, specific information pertaining to production as related to specific stocking rates or degrees of forage utilization is limited. Zertuche (1970) did not find a significant difference in daily goat gains between stocking rates of 7 and 14 head per 5 hectares in a mixed shrub-grass range in Mexico. Shelton (1961) found that low fertility in the Angora is largely related to overstocking. Carrera (1971) stated that overstocking is a major contributing factor to low levels of production in northern Mexico. Malechek (1970) reported

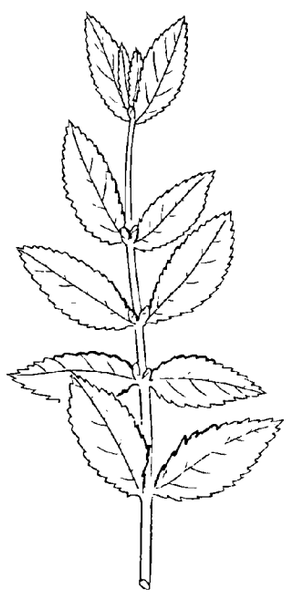
1-year results of a study being conducted on the Texas A&M University Agricultural Research Station, Sonora, Texas. There, goats in a lightly grazed pasture gained an average of 20.5 lb. per head, compared to a gain of 9.2 lb. per head in a heavily grazed pasture. Merrill and Miller (1961) showed no economical benefits for stocking cattle and goats and for stocking cattle, sheep, and goats at 48 animal units per 640 acres as compared to 32 animal units. It has been recommended that goats be grazed in rotation, but this was based more upon conservation of pasture than effect upon goat production (USDA 1929). Palazón (1953) recommended a grazing rotation in which cattle and horses would be followed by goats and sheep.

The goat's beneficial effects upon vegetation

The goat's use of shrubs as forage has a beneficial effect upon the vegetation. For example, Magee (1957) made an economic evaluation of 15 ranches where goats were used to control sprouts on cleared land of the Grand Prairie in Texas. He found that goats not only prevented or retarded regeneration, but paid for the original cost of clearing as well.

An earlier reference pertaining to the use of goats for shrub control published by the USDA in 1929 reports that goats were introduced into the United States in the middle 1800's because: "They not only furnish a cash return to the farmers, through the sale of mohair and meat, but they can be of considerable value in keeping down sprout growth... ." Gray (1959) stated that goats had been used successfully to control brush on the Edwards Plateau of Texas, and Darrow and McCully (1959) recommended that goats be used as an adjunct to other methods of controlling oak brush in Texas.

Kennan and others (1955), West (1958), and Myre (1958) suggested among other means, that intensive use of goats might be a more effective and economical alternative for controlling brush than herbicides in Central Africa. In Nigeria, it is believed that man must be willing and able to cope with brush invasion before he eliminates the goat (FAO 1966).



Selectivity of shrubs by various kinds of animals

Leo B. Merrill

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Nearly all shrub and tree species are consumed at some time by livestock or big game species. However, the soft-leaved, low-growing genera of shrubs appear to be most preferred. The least desirable appear to be the waxy-leaved shrubs and the conifers. Examples of notably palatable genera native to the Western United States are forestiers (*Forestiera*), serviceberry (*Amelanchier*), birch (*Betula*), hackberry (*Celtis*), mountain mahogany (*Cercocarpus*), bitterbrush (*Purshia*), sumac (*Rhus*), dalea (*Dalea*), and kidneywood (*Eysenhardtia*). Probably less palatable but providing the most browse forage because of availability are oak (*Quercus*), saltbush (*Atriplex*), sagebrush (*Artemisia*), willow (*Salix*), and others of a similar nature.

The concept that big game and goats survive primarily on shrubs, sheep on forbs, and cattle on grass has in most instances been dropped from the rule book. Studies have also shown that various combinations of circumstances can cause severe competition for any forage species between any two or among all kinds of grazing or browsing animals.

Factors influencing grazing

Important factors that influence grazing of various species are: season of use; forest or shrubland disturbance; shading; rainfall and drought; range site and vegetative composition; and rate of stocking and kinds of animals that graze. Though all these factors are closely interrelated, we treat them separately here.

Season of use

This determinant in the use of shrub and trees species is especially important in regions having long, cold winters. During cold periods, there is little growth of forbs or grasses; consequently, big game species, sheep, and cattle are forced to consume shrub and tree species, since these comprise the primary forages available. Shrub consumption on winter ranges varies widely depending upon the location of the site and the kind of grazing animal. Sheep grazing in the salt-desert shrub type have been shown to consume roughly 50 percent browse and 50 percent grass (Harris and others 1951). Other investigators have found a wide variation in shrub consumption on winter ranges (Cook and Harris 1950a, b; Cook and others 1951). These variations were probably due to varying rainfall, temperature, time of sampling, site of interrelationship, or other conditions.

Usually the use of forbs and grass declined during winter; use of shrubs and trees increased correspondingly (Bayless 1969; Hunt and Mangus 1954; McKean 1954). In some

areas, use of shrubs by big game was consistently high. In one area, moose were almost completely dependent on shrubs throughout the year, with less than 2 percent of forbs or grass being consumed at any time (Dorn 1970).

Forest or shrubland disturbance

Disturbance in forest stands generally results in increased use of shrubs by various kinds of animals. Burning opens up a coniferous forest stand and permits invasion or release of shrubby plant species that are more palatable to deer or other species grazing the particular area. Shrub foliage, after burning, is both more abundant and more palatable than that in the original timber stand (Leopold 1950). Burning appears to have the same effect in savannah, where resprouting following burning not only increased amount of plant material available to animals but also increased its palatability (Vogel 1965).

Improved palatability and increased plant nutrients of shrubs following burning appear to be centered in the resprouting portions of the plants. Research has shown an increase in crude protein in resprouted, burned shrubs as compared to older growth of the same species (Einarsen 1946). Also, protein, NFE, and ether extract were more abundant in shrubs than in bluestem grasses (Dalrymple and others 1965).

Browsing of shrubs also appears to improve the nutritive value of the plants. The nutritive value of regrowth plant material is higher than that in unbrowsed twigs (Reynolds and Sampson 1943).

Chemical spraying from aircraft, which reduces forest stands, generally has the effect of improving grazing on understory shrubs. Usually, spraying oak woodland, as well as certain savannahs, increases shrubs preferred by animals. (Dalrymple and others 1965; Elwell 1964; Halls and Crawford 1965). Spraying has also released understory pines; this increased herbage production, at least for a time, in the Central States forest (Ehrenreich 1959). Burke (1956) pointed out that improving good timber stands results in increased deer numbers.

Shading in forest stands

The above discussion of effects of disturbance has assumed that the favorable response in improved nutritive content and palatability of shrubby vegetation was due to regrowth of sprouts following spraying or burning. This disturbance first killed back shrubby plants causing resprouting. Reduced competition permitted more rapid and vigorous plant growth and thus increased both foliage and palatability. Closely interrelated with this response is the effect of shading. Some plant species grow satisfactorily under moderate shade, but they are grazed very little and generally only when the grazing animals are under food stress. Such plants apparently are low in palatability, but there is considerable controversy regarding the exact cause of the condition. One study has shown that plants grown in the open have greater sugar content than those grown in shade (Welton and Harris 1928). Another showed that plants grown in the open had a higher NFE content and lower crude fiber content than those grown in the shade, but the plants grown in the shade had more crude protein, calcium, and phosphorus (McEwen and Deitz 1965). This would indicate that palatability of plants grown in the open is closely related to sugar content and lack of crude fiber.

Range site and vegetative composition

It is well known that range site strongly influences the species of plants that grow in a particular region. This characteristic of site influence is found throughout the world. On the Edwards Plateau in Texas, *Quercus virginiana* occupies rocky sites with deep soil between rocks, while *Quercus pungens* grows on shallow, rocky sites. The vegetative composition breaks sharply with the site change. *Purshia tridentata*

and other palatable shrub species are found on one site in Oregon but are not found on an adjoining site (Anderson 1955).

The palatability of one plant species is strongly influenced by the availability of other palatable species growing with it (Crouch 1968; Klebenow 1915).

Such factors as rainfall, temperature, plant competition, and past grazing use influence vegetation composition. These same factors and stage of maturity influence consumption of various species (Cook and Harris 1950b). This combination of factors brought about an interesting variation in the use of browse plants on the Edwards Plateau. Observation on the Kerr Wildlife study near Kerrville, Texas, showed that deer alone on a completely enclosed pasture browsed several oak species and even juniper, leaving a browse line 5 to 6 feet high (McMahan; McMahan and Ramsey 1965). At the same time, studies on the Sonora Research Station showed that a similar number of deer, even in the presence of livestock (cattle, sheep, and goats) did not create such a browse line (Merrill and others 1957). The two areas, approximately 80 miles apart, are both in the limestone region and have the same range sites. The primary difference appeared to be fewer forb species in the Kerrville area. Browse composition and density were similar on the two areas. Competition for the shrubs was much greater in the Kerrville area, where only deer were present, than in the Sonora area, where both deer and livestock were present.

The Sonora area has less rainfall and shorter grass species. These shorter grasses compete less with forbs than do the taller grasses found near Kerrville. The grazing pressure of cattle, sheep, and goats in the Kerrville area has also been much more intensive over the years than at Sonora and could have resulted in fewer forbs now found near Kerrville.

Rainfall and drought

Rainfall and drought directly affect forage yields and grazing pressures on various range sites. But since rainfall, or lack of it, plays such an important role in the utilization of less palatable browse plants, it is treated separately here. Browse species furnish livestock foliage during drought, when there is little or no grass growth.

The Edwards Plateau is an excellent example of this. Since grazing pressures by cattle, sheep, and goats are always great, generally exceeding 50 animal units per section, and since foliage production from grass and weeds is always critical, a short drought sharply reduces the forage supply from grass and forces both livestock and deer (which also occupy the range at concentrations of roughly one deer to 3 to 18 acres) to subsist largely on browse. Under such conditions of stress, all genera of shrubs are utilized frequently to a height of 6 feet or more. Shrubs not only furnish emergency forage under such conditions but provide a relatively high quality feed as well. Shrubs generally contain more protein than grasses and forbs; also, shrubs retain their protein, carotene, and carbohydrates better during drought than either grasses or forbs (Stoddart and Smith 1955).

Rate of stocking and kinds of animals grazed

The rate of stocking of native ranges by either domestic livestock or big game is probably the single most important factor in determination of shrub usage. Heavy grazing by domestic animals leads to reduced forage production from preferred plant species; this causes the animals to alter their grazing patterns to include progressively less palatable species until the final stages of range abuse force the utilization of all species. Even before severe range damage, intensive grazing causes most shrubs and trees to be grazed (Casady and others 1955; Cory 1927; Julander 1951; Merrill and others 1957). With moderate grazing rates, most palatable shrubs are utilized if appreciable numbers of either deer or goats are present but use is relatively light as long as herbaceous vegetation is available. Shrubs comprise 10 to 16 percent of

cattle diets (Halls and others 1957). Under moderate use by cattle and deer, deer graze most desired shrub genera (i.e., *Forestiera, Celtis, Rhus, Eysenhardtia, Dalea,* and others) without severely damaging the shrubs if forbs and other desirable forage are available (Martinka 1968). In this case, use of more abundant and somewhat less preferred genera such as *Quercus* will be rather light (Merrill and others 1957). If forbs and palatable grass are not available, then deer destroy preferred shrubs and browse excessively on less preferred shrubs (McMahan 1961; McMahan and Ramsey 1965). Goats alone at moderate continuous stocking rates exert continuous browsing pressure on even moderately desirable shrubs and lead to damage of these shrubs along with reduced foliage production (Malachek 1970; McMahan 1961; McMahan and Ramsey 1965; Merrill and others 1957).

Light stocking rates of domestic livestock permit most desirable shrubs to develop; but even light stocking of goats alone places stress on the most desirable shrubs (Merrill and others 1957). If deer are added at light rates of grazing by domestic livestock or if numerous deer are grazed alone, damage to some shrubs may be expected (Maloiy and Heady 1965; McMahan and Ramsey 1965; Nellis and Ross 1969). Deer densities of 14 per square mile permit shrub development in the Adirondacks, but densities of 27 per square mile repress shrub development (Behrend and Patric 1969). In many areas shrub development continues despite heavy grazing use; but the shrubs will be less palatable though they may contain more crude protein than grasses (Maloiy and Heady 1965). It appears that the most damaging result of heavy grazing is a decrease in the quantity of foliage, followed by decreased intake by foraging animals (Cook and others 1965).

The preference that a given animal shows for any particular species of plant will not necessarily be repeated. The flora of any area is constantly affected by several factors that have been mentioned already or by interactions between several or all of these factors plus others. It is therefore difficult to list plant genera or species in ranked order of palatability. The order is likely to change from one period to another. However, particular kinds of animals consistently prefer certain plant species for food.

Conclusions

Nearly all shrub and tree species are consumed at some time or under certain conditions by livestock and big game. Animals usually prefer soft-leaved, low-growing shrubs.

Important factors influencing grazing of various species are: season of use, forest or shrubland disturbance, shading, rainfall, range site and vegetative composition, and grazing use and animal composition.

The most palatable shrubs are grazed during their growing season even in presence of palatable forbs. Species having low palatability, such as the conifers, are generally grazed most heavily in winter or under severe stress when forbs and more palatable browse foliage are not available.

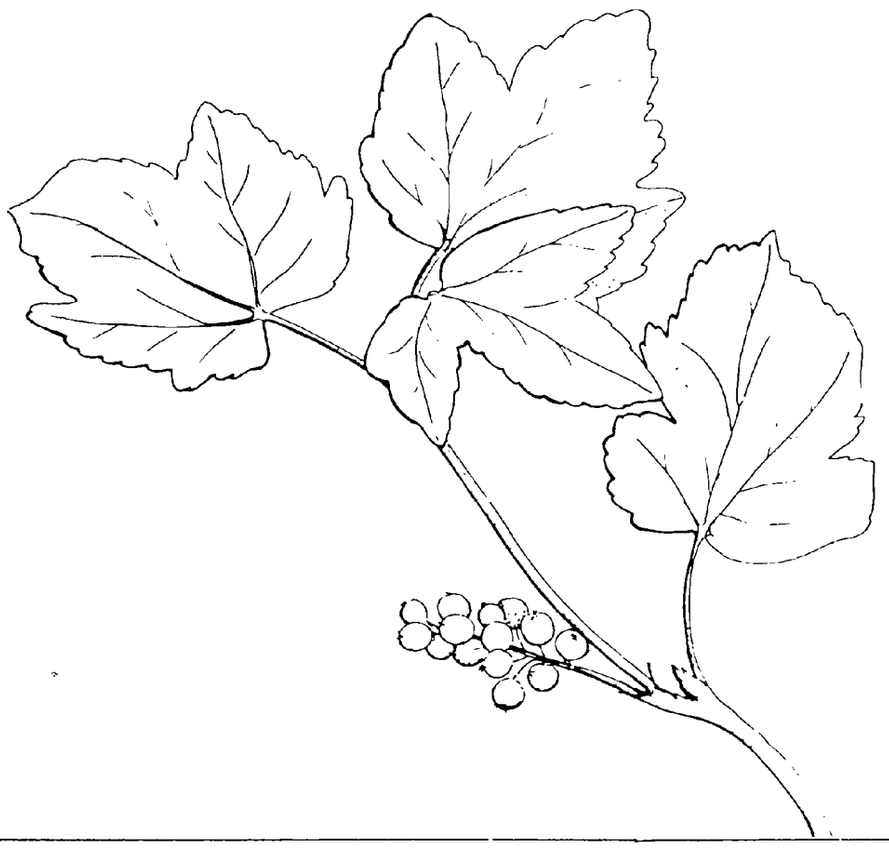
Any disturbance that opens up a forest stand increases the amount and palatability of shrub foliage. Reduction of shading leads to increased palatability of shrubs. Range sites and various factors that affect vegetation composition of those sites lead to a variation in palatability of any given species of shrub. The relative palatability of a shrub species is frequently dependent upon the presence of other plant species.

Drought has a marked effect on shrub usage in that shrubs in general produce more foliage than grasses or forbs during drought and their nutrient content is usually higher.

Heavy stocking of goats, deer, or sheep usually leads to utilization of most shrub species on any given area. Continuous heavy stocking is most destructive to shrubs when grazing animals are goats, followed in declining order by deer, sheep, and cattle.

Section VII.

Regeneration



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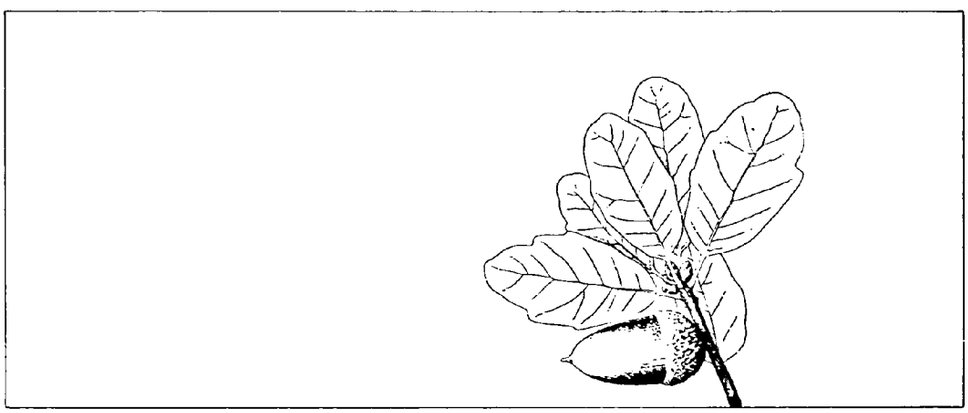

Shrub seed production

Clyde Robin

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Individuals who collect, clean, and sell seed are known as seed collectors. Most are hobbyists who have a love for plants.

One of the early influential California collectors was Theodore Paine whose collection, promotion, and sale of seeds and plants began just after 1900 and extended to the early 1950's. Closely following Paine was Lester Rountree--a dynamic writer and lecturer as well as a collector and seller of native seeds; his activities spanned from 1920 until the early 1950's. Rountree wrote:

> If you can sleep on the ground, subsist on nature's fruits and berries, arise with the dawn, endure the desert's heat, tolerate gnats, fleas, flies and ants, dust, pollen and itching fuzz of seeds, husks and plants; if the chill of the mountain rain in the night as it descends on your tired hungry body doesn't daunt you, if you can run your hand lightly, deftly, and lovingly over a plant and gather a handful of seed, if you can lock yourself away from the world and live and respect nature as your only companion, if you can endure these things and love your lot more each day, you will be a seed collector.

I had been collecting seeds as a hobby for many years before I started my mail-order business in the early 1950's. Collecting in those days was often done by tying a sack around a plant and leaving the sack on until the plant shed the seed.

The work of early plant lovers evolved into a movement that drastically changed native seed-collecting methods. About 1915, a number of studies began; during the 1920's, various universities and government agencies began shelterbelt studies. These studies increased during the 1930's and "shelterbelts" gained more recognition during the "dust bowl 30's." As these studies continued, public interest increased; during the late 1940's, various organizations began to inquire about sources of native seeds. In 1939, "Native Woody Plants of the United States, their Erosion Control and Wildlife Values" was published by the U.S. Department of Agriculture. In 1948, the U.S. Department of Agriculture published the "Woody Plant Seed Manual" which listed many plants; for most, it included seed collection and storage information.

In the 1950's, highway departments began to broadcast native seed for landscaping and erosion control. Architects for housing projects began to specify native plants for erosion control. Self-proclaimed naturalists became involved in planning, constructing, and planting native gardens. It was the "thing" to do.

The publication "Restoring Big Game Range in Utah" by A. Perry Plummer, Donald R. Christensen, and Stephen B. Monson is an invaluable publication. It lists the shrub, cost per pound, acceptable purity, number of seeds per pound, and maturity dates as well as other information. Although 3 years old, the seed costs cited in this publication are still quite close to costs. The distribution of this publication has helped reduce overpricing. The tendency today is toward standardized pricing--prices that reflect the total cost involved in seed production.

Hand-collection methods are recommended in the "Woody Plant Seed Manual." Collection and cleaning information for 44 of the 52 shrubs listed is available in "Restoring Big Game Range in Utah." Of these, only one is not collected by hand; this is collected by vacuum, which requires four men as are also required for hand collection. It is questionable that the amounts collected by vacuum are any greater than the amounts collected by hand. Eight different methods are listed for the collection of the 44 species. Several types of seeds can be collected using one method; we collect several seeds using one machine. We have developed several successful seed machines each of which can be used to collect more than one species.

Presently seed harvesting of native shrubs appears to have branched into several well-defined patterns. Because harvesting of native seeds is a seasonal operation, it has attracted students seeking summer work. These students often are attracted by the prospect of financial gains and have entered the collecting field before they were sufficiently mature. Sometimes lack of judgment caused them to secure the wrong seed, collect inferior seed, mislabel seed, or become involved in other indiscretions. Sometimes the seed collector collects for himself as well as employing others to help him.

Some collectors sell the seed at spot or bid prices; others may establish prices; some like to bargain. Sometimes large inventories force collectors to lower prices to obtain needed funds. Such collectors usually have considerable investments in seeds and equipment. All attempt to refrain from building inventories so as to avoid the need for dumping the overaged seeds. When a collector does not have seed on hand, he often loses business if a specific seed is ordered, so it becomes a matter of judgment in choosing which course to follow.

Presently, seed collectors sell seeds to branches of the federal and State governments, county agencies, and--to a lesser degree- to cities, corporations, and private individuals. Federal and State governmental agencies often have seed banks that are "fed" by seed purchased from individuals and seed that the agency's personnel collect, process, and store.

The problems of the seed producer will continue to increase. In 1948, the "Woody Plant Seed Manual" listed certain standards of seed purity and germination for some native shrubs. Since that time, many other publications including Plummer's work have added to this list. It is now standard procedure for purchasers to specify seed purity and germination standards. Sometimes they also specify that seed come from given areas and from given soil types. Not only are these specifications being spelled out, but they are beginning to be enforced.

Studies have been made on ecotypes within a species. There is ample evidence that superior types of shrubs can be developed based on soils, elevation, and climatic areas. Some purchasers are beginning to request superior types of seeds. They want to know location, altitude, and date when seed was gathered, as well as the purity and germination.

Many research organizations find it impossible to secure from collectors all of the types of seeds they need; as a consequence, they collect their own seed. These organizations have probably been the leaders in discovering techniques for collecting,

cleaning, and storing of seed. They have trained many of the most efficient collectors in the business. Their purchasers stimulate the market; at the same time, they tend to stabilize it. If private collectors are to supply seeds for this new and growing market, they must become knowledgeable in the field of plant selection. This requires a continual learning process for the collector, if he is to keep abreast of the continuing flow of new information and identification requirements.

Fortunately, most native seeds require very little special treatment for storage, but viability of most seeds is retained best when temperature and humidity are controlled. Collectors need better knowledge about labeling, packaging, and shipping--whether they are selling intrastate or interstate, or to buyers in foreign countries. Such sales often require knowledge of quarantine laws and inspection procedures by government agencies at the county, State, federal, and foreign levels. Formerly, native seeds were exempt from some of these requirements, but they are now coming under careful scrutiny.

It is evident that the collector is faced with all normal price increases plus a few special increases peculiar to his work. It seems that the larger collectors are destined to take their places as businessmen, paying taxes, wages, benefits, and having more restrictions placed upon them. They, of necessity, must collect more and better seed. They must improve their cleaning, storage, and shipping methods. They must employ full-time workers and keep better records.

As the producers of native seeds are being confronted by rising requirements and costs, the users of such seeds are often being controlled by budgets that do not rise as fast as producer costs. Some adjustments probably can be made to bridge the gap in cost differential between producer and user.

Areas that are satisfactory for propagation of a given shrub and that are located within public lands could be reserved by the Bureau of Land Management, or other appropriate agencies, as growing grounds for particular shrubs adaptable to these specific areas. Superior strains of a shrub could then be introduced to a specific area and/or other areas in amounts capable of producing sufficient seed of that particular type for the needs of all agencies using that particular seed. To insure against crop failures, alternate lands could be used, at least, in some areas. In others, irrigation of shrubs would insure and possibly increase the yield of seeds. The use of such artificial introduction of superior shrubs would concentrate stands and reduce travel and resultant collection costs. There is a good possibility that such plant introductions could be planted in a pattern that would lend itself to mechanical harvesting. Whether governmental agencies introduce shrubs to these areas for their own use or for use by private producers would not measurably affect the end result. The seed would be produced.

The Bureau of Land Management should explore this possibility in cooperation with other governmental agencies. The public owners of public lands would benefit; furthermore, this would be a prudent use of the land. Land that can be watered and machine harvested should be secured. I believe appropriate land could be found in every plant zone.

What I have said about public lands could be said about public highways with slight modifications. They occupy thousands of acres often of prime land having accessible water. Such highways, too, are found in every plant zone. The public is clamoring for use of native shrubs in landscaping; let us do so. Such plantings could be done attractively and in such a manner as to permit a mechanical harvest.

There is a third alternative for superior shrub seed production. Rising land costs and increasing taxes have increased the operating costs on marginal lands beyond the potential income of such lands. Some sizable tracts, formerly profitable cattle

ranches, are now a burden to the owners. Some of these ranches are located in prime shrub country. They are several square miles in area and have water for a few acres. They can be obtained at below appraisal prices. They contain level and rolling land suitable for machine harvest and have several hundred species of plants growing on them at this time. The soil is porous and of good quality. A variety of shrubs certainly could be introduced.

In any of these options, and probably others, some breeding control on an adequate scale could be accomplished. A superior type of shrub could be cultivated and disseminated over a wide area. Considerable machine harvesting could be done; in terms of the third alternative, threshing and storage could be easily accomplished. An even flow of seeds would be more possible than at the present time.

From observation of the emergence of a seed-gathering hobby into a full-time occupation, I feel that managers of public lands and their suppliers of seeds are moving toward better control of nature's resources. They are rapidly improving the grazing for game. Their experiments of the past have produced valuable knowledge that is now being applied with good results.

Propagation of shrubs in the nursery

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The propagation of useful wildland shrubs in a nursery is no different from that required for any other shrub. Seedlings or asexual reproduction can be used. But a wildland shrub nursery is more like a forest tree nursery than an ornamental operation; usually propagation is by means of seeds.

Nursery practices appear to remain an art since scientific investigation still is confined to specific physiological responses and does not, at this point in time, consider overall organization. *The Modern Nursery* by Laurie and Chadwick (1931) seems to be the latest comprehensive treatise on the subject. An even older work (about 1907), *The Nursery Manual*, by L. H. Bailey, has been reprinted (1967) to fill the gap. Hartman and Kester have published *Plant Propagation Principles and Practices* (1959), but it lacks details on nursery management. Possibly the newest work is that of Patterson (1969), *Container Growing*. Yet the skills of propagation methods and practices are highly developed and widely employed.

Nursery practices, however, are well represented in older literature. Some works as old as Loudon (1844) contain very practical and up-to-date procedures that need only to be put into a modern setting of methods, using the mechanical devices and chemicals of today.

Practices include land preparation, fertilizing, seeding, watering, weeding, disease and insect control, and the like. These subjects are better referenced in texts on irrigation, cultivation, disease and insect control, fertilizing, etc., than they are in most horticultural literature. A little "borrowing" is necessary. Both Bailey (1935) and Taylor (1941-42) give general cultural directions for a host of plants. The *Woody Plant Seed Manual* (1948) is the closest to the subject at hand, but it too is limited in scope, particularly with regard to nursery practices. *Tree Planters Notes* beginning in 1950 and now (1971) in the 22d volume, offers some of the best information for carrying out large-scale nursery practices with nonornamentals.

General considerations in nursery operations

Site

A nursery *site* must serve a region. One may be able to predict or discover which is a useful wildland shrub by observing it in its native locality. The experience the Soil Conservation Service has acquired, however, shows clearly that while one particular variety of a species may not be desirable, others of the same species may be both desirable and reproducible.

Some sort of a testing program is therefore necessary. Testing should be carried out in the general climatic range where the shrub grows or is expected to be used--if possible, also on the same sort of land resource area. The final test will be the plant's performance on the desired site.

Site selection is of great importance. The soil needs to be workable under a variety of moisture conditions. The land should not be subject to erosion. This usually means the best flat but well-drained land in the region. Soil amendments and water can be supplied, but if weeding, lifting, or other operations cannot be carried out because of wetness or dryness, there is trouble. Soil surveys are available or can be made on which site selections can be based (Bartelli and others 1966).

Water

Water quality is important. Irrigation is essential for nurseries where seedling or certain other classes of stocks are raised. Lack of enough water at a critical period can result in failure. If the water is saline, the supply should be plentiful and the soil sufficiently permeable to permit leaching and prevent excessive accumulation of salt.

Planting and lifting operations

Mechanical equipment is required in every phase of outdoor operation. There are machines available for almost any nursery operation. Planting arrangements should be coordinated with equipment. Too often we see bed or row arrangements made that do not fit the lifting equipment.

Innovation can also be important. An example is a Soil Conservation Service nursery remodeled tractor-cultivator to handle three rows instead of the two for which it was designed. This innovation removes the edge effect in standard 6-foot beds and at the same time conserves valuable irrigated land. With this particular crop (kudzu), 6-foot beds, regardless of the number of rows, provided only the number of seedlings per acre that could be secured in standard 3-foot rows. By discarding the bed and using 2-foot rows, the per-acre production was increased by one-third. In the final analysis, a nursery operator must know his crop and adapt his equipment to his crop.

Pesticides

Herbicides have received much attention in nursery operations recently. Attention has been given to a range of herbicidal forms, sterilants like methyl bromide, depressants like maleic hydrozide, and selectives like the group generally called "preemerge." Most of them have the primary purpose of reducing weeding costs. This field of activity is one of rapid change. Some phases of herbicidal weed control will probably be necessary in any sizable nursery operation. Various periodicals frequently publish herbicidal guides. One recent one is the *1970 Weed Control Guide and Herbicide Manual.*

When growing shrubs, a great many herbicidal transfers can be made with relatively simple tests. For example, preemergence chemicals worked out for such crops as peanuts

and soybeans can be used on most leguminous plants with minor adaptations. Buchaman and Burns (1969) show this for *Sericea lespedeza*. The Soil Conservation Service in its plant materials centers is currently using adaptations of Buchaman and Burns' procedures to produce bristly locust, woody lespedezas, desmodiums, kudzu, etc.

Useful wildland plants must have a degree of pest and disease resistance. In the wild, the necessary resistance is present. It does not necessarily follow that the nursery will be free from disease. Damping-off is one of the principal causes of loss in seedlings. Other diseases, and sometimes insects, will build up to epidemic proportions where there is a concentration of plants that otherwise would be incidental. These diseases and insects will have to be controlled.

Seed source

Useful wildland shrubs may or may not be commercial items. When commercial, most of them will be grown only infrequently. For example, *Amorpha fruticosa* (indigobush) is useful in controlling erosion on dams and in stream channels. It is also valuable for wildlife food. It is a listed trade item, as an ornamental, but often difficult to find. However, indigobush is easily and more cheaply grown from seed, and seedlings are easily transplanted as 1-year-old barerooted stock. But seed is not available commercially. Commercial stock is usually produced by rooted cuttings from a clone at greater expense than seedlings.

To insure success with such a plant, costs must be considered. And, since seedlings are cheaper, a seed source will have to be developed. This may require the establishment of a commercial collection facility or the establishment of a seed orchard.

Seed cleaning

Facilities will be needed for cleaning and treating the seed: dehulling, dewinging, macerating, depulping, and removing trash. While a small-scale operation can be carried out with crude methods and without too many refinements, large-scale operations should be handled mechanically to produce a uniform, high quality product.

Seed storage

Some seed, like *Amorpha*, can be stored for long periods; others cannot. In any event, modern seed storage facilities, providing for both temperature and humidity control, are necessary.

Seed treatment

Many seeds have dormancy problems of one sort or another. Some require mechanical treatment, others respond to chemical treatment, and yet others to stratification. Equipment, supplies, and facilities must cope with these problems.

Stratification is the most common treatment practiced for germinating seed. It can be accomplished for most plants by fall seeding in their native region. This practice is a waste of space for a species that requires 2 years to germinate. It also demands a higher rate of seeding for loss caused by rodents and weather. Now stratification can be accomplished by using the cold storage process. Seed bags now used in the cold storage process permit water and air to enter. The bags are arranged so that the wetting medium (sphagnum) is kept from the seed. This allows for mechanical planting of the seed when it is ready without the necessity of another cleaning or the sowing of more bulk than necessary. In temperate regions, wet cold storage is needed for this kind of operation. In the tropics, lathhouses for shade and frequently mist spraying are often used. The older practice of mixing seed with sand or other mediums has for the most part been discarded.

Container growing

Container growing is becoming more popular and is a practice requiring some shade and an abundance of water. This practice makes it easy to handle species that are difficult to transplant and makes it easier to establish plants in critical sites. People who buy and use such plants prefer them in containers.

Asexual propagation

Seed is not the only means of propagation. Most plants lend themselves to some form of vegetative increase. In the discovery and developing of useful wildland shrubs, it has been demonstrated that some ecotypes are better suited for a particular use than others. It is frequently necessary to propagate such plants asexually to establish foundation source. Other plants, too, for reasons of expediency or to maintain genetic materials may be reproduced asexually. Some plants require asexual propagation because of lack of viable seed. Asexual reproduction facilities, such as mist beds for rooting cuttings, cold frames, and grafting beds, will be useful.

The Los Lunas plant materials center

The following material provides a good picture of how one specific plant materials center finds wildland shrubs, tests them, and puts them into use. It is perhaps a better way of pointing up the opportunities and problems. At the Plant Materials Center, Los Lunas, New Mexico,[1] SCS is collecting, growing, and testing native and exotic woody shrubs for highway erosion control, beautification of native and naturalized areas, and for wildlife habitat improvement.

Assembly

The propagation of previously uncultivated wildland shrubs begins with the collection and assembly of as many sources of seed, live plants, or scion wood as needed to make evaluations, provide plant materials for continued evaluation, or establish an arboretum of selected materials for seed or vegetative production.

Plants and seed are cataloged, listing time and place of collection, the collector, and giving any pertinent information on site, soils, elevation, and use by wildlife or livestock. Each collection is given an accession number.

Testing

Plant materials are grouped for testing according to their uses such as ground cover, browse, barrier shrubs, etc. There are usually two categories in any use group. The first category is comprised of native shrubs endemic to the area served by the plant materials center. Ordinarily, detailed knowledge of the geographic areas of adaptation, soil-plant correlations, climatic adaptation, and much other ecological data is known. Supplies of seed collectible for testing are adequate and techniques for germination and establishment are known.

In this category, the number of plants desired and the type and place for continued evaluation plantings can be developed early in the testing phase. Evaluation may center around finding a superior strain to establish a seed orchard. This will provide a continuing source of high quality seed for propagation of nursery stock or for direct seeding at the planting site.

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[1]The Los Lunas Plant Materials Center is located at the Middle Rio Grande Branch Experiment Station, Los Lunas, N.M., and is operated cooperatively by the USDA Soil Conservation Service, Albuquerque, N.M., and the New Mexico State University Experiment Station, Las Cruces, N.M.

This work is usually carried out at the plant materials center using small plots under overhead sprinkler irrigation. As many sources of seed as can be assembled at any one time are included in the test. When available, a previously grown accession is included for comparison. The plants are evaluated on the center for the characteristics needed for the intended use.

Enough seed of each accession is planted so that several hundred live plants will result. The number needed will depend upon the amount of off-the-center field evaluation plantings to be made in any one year and the space and equipment available for storing live plant materials through a planting season or over a period of years.

The second category is the group of plants for which limited amounts of seed are available, techniques for germinating seed or vegetatively establishing plants are not known, or only general information on geographic, edaphic, and climatic adaptations is available.

These materials often are started in the greenhouse and lined out in the field. The first task may be to find the proper method of planting to achieve germination and seedling establishment.

Because it is often difficult or impossible to collect additional seed of a particular accession, the next step is to develop these plants into a seed source. It may take 3 to 5 years or more before the plants become mature enough to produce viable seed. So, testing may have to be delayed for a time.

For this category, a long period of field evaluation will usually be required, including the production of a specified amount of material each year to meet the testing needs. Larger numbers of plants of more accessions will be required than for the plants in the first category.

Seed supplies for testing

Establishment of seed sources for promising accessions assumes primary importance early in testing. Unless larger than usual initial seed collections are made, supplies of seed for production of live plants over the several-year period needed to evaluate performance in the field will usually become a critically limiting factor. Although many of the poorly performing accessions in the initial tests of a species are eliminated, several of each usually are kept. Through a process of selectivity, less desirable accessions are cast aside and the better plants established in an arboretum or seed orchard as soon as possible. They are cultivated and grown as rapidly as possible to get them to the seed production stage.

Propagation of shrubs in sprinkler beds

Most of our shrubs are propagated in open beds under overhead sprinkler irrigation. A five-section system is used. One section may be planted to shrubs that will remain under observation for up to 3 years. Since only a portion of all materials will be under observation for this long a period, the remainder of the bed will be planted to stock which will be dug off at 1- and 2-year intervals. Parts of the beds are replanted each year to stock dug off at 1/0 age.

The remaining four sections or portions of these sections are in a soil improvement program. They are fertilized with cow manure and put into a continuous rye-sudan green manure rotation for 2 to 3 years.

A major problem that we have is in keeping salt concentrations within tolerable levels. All the overhead irrigated sections have poor subsoil drainage. After a period of 10 years of continuous use with water that contains about 1,500 pounds of soluble salts per acre-foot, we have developed salt levels which are physiologically damaging to plants of low salt tolerance. Drain laterals will have to be installed and the soil leached along with the continued use of the manure-green manure crop rotation in order to improve this condition.

Shrubs are seeded at two times of the year: late fall (early winter) or early May. Those species or accessions requiring mild cold stratification to break seed dormancy are seeded into beds in the late fall or early winter. Beds are mulched with excelsior blankets, and the soil is kept moist to the surface. At Los Lunas, some shrubs begin to emerge in early February from these fall plantings.

Species that will germinate readily or that require treatments other than mild cold stratification such as long cold treatment, acid scarification, hot water treatment, or soaking in cold water to break seed dormancy are given these treatments indoors and then planted in early May.

Spring planted beds are also mulched. In the past, burlap and hay mulch or hay mulch alone has been used. When burlap is used, it is essential that daily checks for emergence be made. The burlap must be removed at the first sign of emerging seedlings. After the mulch is removed, shade frames of snow fence are usually installed. In general, the excelsior blanket has proved to be an adequate mulch for all species we have tested except the junipers. The seedlings will emerge and grow through the mulch, which can be left intact on the beds throughout the growing season. It will rot and be sufficiently decomposed by the next spring for plants to be dug without interference from the mulch. Usually, however, the mulch is rolled off the beds after the seedlings have emerged to facilitate weeding. This can be done easily with little or no damage to the seedlings. Shade frames help protect many of the species from wind. They aid production, particularly when soil salts are a problem by reducing evaporation.

Seed is planted in one to five rows in each 48-inch bed depending upon the plans for use of the material. Usually three sizes of material are handled at the Los Lunas Plant Materials Center. Large plants are shipped bare root, medium-sized plants are potted in gallon cans, and small plants are potted in 2 1/2- by 2 1/2- by 9-inch tarpaper pots. Table 1 lists some of the ways used to establish row spacing when planting shrubs based on the size of plant which can be used in the program.

Plants such as willows and cottonwoods are often started from cuttings in the sprinkler beds. Scion wood is cut in the late winter or early spring while still dormant. The cuttings are made from good healthy wood and are approximately 6 to 8 inches long. They are covered with moist sphagnum moss and wrapped in black polyethylene film. The packages of cuttings are stored in the refrigerator at 33° to 38° F. until all danger of frost has passed.

The cuttings are set in the bottom of a shallow furrow, and the furrow is filled with vermiculite or sawdust to mulch the cuttings. They are then watered with overhead sprinkler lines as needed to keep the soil and mulch moist.

Insecticides and fertilizers are applied as needed. Water is used liberally. Weeding is done by hand, with a rototiller, or in larger areas with a disk harrow. Notes are kept on performance from emergence until the plants are dug and processed.

Table 1.--*Number of rows planted per 48-inch bed*

Seedling growth rate	Use	Age harvested	Row spacing
Slow	Bare root	1/0	1 row
Slow	Bare root	2/0	2 row
Slow	Pots[1]	1/0	2 row
Slow	Pots	2/0	4 row[2]
Medium	Bare root	1/0	1 row
Medium	Bare root	2/0	4 row[2]
Fast	Bare root	1/0	2 row
Fast	Pots[1]	1/0	5 row[2]

[1] 2½- by 2½- by 9-inch tarpaper pots and 1-gallon cans.

[2] Edge effect results in the outside rows growing more robust, larger plants in the outside rows and small to intermediate plants in the inner rows. Thus, three sizes of material can be sorted from one bed; however, material from the outside rows will not be as large as if grown in one or two rows per bed.

Processing shrubs grown in open beds under sprinkler irrigation

Plants are dug any time in the late winter or early spring before the first species begin to break dormancy and after the frost leaves the ground. A tractor-mounted blade which lifts and loosens the soil around the roots is used to dig entire beds. When only the outside rows are dug, they are dug by hand with flat-bottomed shovels.

Plants are immediately lifted from the soil and wrapped in moist burlap. They are transported to the sorting barn, and the burlap moistened and covered with tarps.

The plants are sorted into three size groups. The small plants are for potting in 2 1/2- by 2 1/2- by 9-inch tarpaper pots. The medium size are those plants too large for tarpaper pots but small enough for 1-gallon cans. Any plants too large for 1-gallon cans are usually shipped bare root or transplanted into seed orchards. In some cases, they will be lined out in fields for continued growth and observation. All unhealthy, diseased plants or plants with bench roots are discarded.

The plants are sorted and tied into bundles and are top pruned and root pruned. The roots are dipped in a slurry of clay soil and water. Moist sphagnum moss, which has been presoaked and run through a handwringer, is placed around the roots, and the bundles are wrapped in black polyethylene film leaving only the tops exposed. The bundles are tagged showing the species, accession number, and distribution. The bundles are then placed in a walk-in refrigerator for cold storage until shipping, planting, or potting takes place.

The humidity of the walk-in cooler is controlled by placing open pans of water inside the cooler or by an occasional misting. The bundles of plants are checked periodically and the sphagnum moss moistened when needed. Temperatures are maintained

at 33° to 38° F. Any plants which have broken dormancy and begun growth prior to digging, particularly the evergreens, will usually continue to grow slowly in the cooler. These will require careful watering to keep the tops viable, since transpiration will occur at a greater rate among these plants than it will on dormant plants.

Preliminary investigations indicate that hardy deciduous shrubs can be held in cold storage for 4 to 6 months following digging with good viability after transplanting, provided reasonable care of the material is taken during processing, storage, and planting. Evergreens require much more exacting and careful handling depending somewhat on the species. Success with evergreens obtained from bare root plantings following cold storage has usually been much poorer than that obtained with deciduous stock.

Potting of shrubs

Potting live plants serves to hold them through a part of the growing season in order to take advantage of the optimum conditions for planting or to hold them over from one growing season to the next without appreciably increasing their size. In some cases, by repotting the material over two or three growing seasons, specimen plants can be obtained. Potting also increases viability when planted.

Two pot sizes are in general use at Los Lunas. The preferred size is the 2 1/2- by 2 1/2- by 9-inch tarpaper pot. Approximately five tarpaper pots can be stored and shipped in the same space as a gallon can. The tarpaper pot does not have to be removed when the plant is planted, and getting uniform drainage is less of a problem with pots than with gallon cans. One disadvantage is the small area available for root development.

Gallon cans have more soil per plant and can accommodate a larger initial root system than can tarpaper pots. Disadvantages are that material stored for more than one growing season becomes potbound and should be root pruned and repotted. The cans must be removed from the plants when the material is transplanted in the field. Gathering and disposing of cans during transplanting requires additional time and effort.

The soil mixture used for potting is equal parts in volume of loamy sand and sawdust. The sawdust is fortified with 1 percent nitrogen by weight, is partially decomposed and has been premoistened before mixing with the sand. This mix has some advantages and some disadvantages. It forms a well-drained soil with good water-holding capacity because of the high organic matter content. Excellent well-branched root systems are developed by plants grown in this soil. The sawdust is an inexpensive source of organic material when compared to other organic materials like sphagnum moss or peat moss or to inorganic materials such as perlite or vermiculite. It is much easier to mix with sand than manure or compost, and has the added advantage of being weed-free. Because the sawdust is acid in reaction, it helps buffer the calcareous soils and salty water at the Los Lunas PMC.

Disadvantages are that inherent fertility is low, particularly nitrogen and phosphorus. The microbial breakdown of sawdust ties up large quantities of available nitrogen, and the high organic matter level ties up the available iron.

Tarpaper pots are formed at the time of potting using 9 by 11-inch squares of 30-pound tar felt. The tarpaper is folded into a form on the potting bench and soil is put in, filling it approximately half full when firmly tamped or pressed. A plant is laid into the form with the crown line about one-half inch below the top edge of the pot. The pot is then filled with soil which is compacted, and the edges of the pot are folded and stapled. The pots are placed in a metal band having a removable bottom. Each band holds 12 pots. The pots are taken to the lathhouse and placed in beds. They will remain there for the growing season.

Using gallon cans, the plants are placed in the cans which have been prepunched with a uniform number of holes of the same dimension so that drainage is generally good and rapid enough to prevent waterlogging. Soil is placed in the cans and the cans placed in beds. The cans are well watered to settle the soil and remove any pockets of air around the roots.

Maintenance of potted stock

Because of the high organic content of the potting soil and its low inherent fertility, a regular program of fertilization is used. As soon as all the plants have resumed growth following potting, a blanket application of 100 pounds per acre of available nitrogen and 100 pounds available P_2O_5 per acre are applied to all beds in the lathhouse.

Additional applications of nitrogen and chelated iron are applied as plant growth indicates the need. This may range from none for such shrubs as *Forestiera neomexicana* Gray (New Mexico forestiera) to as much as 300 additional pounds per acre of available nitrogen on *Cercocarpus montanus* Raf. (mountain mahogany) and *Amelanchier alnifolia* Nutt. (common serviceberry).

The objective of the fertilizer program is to maintain good healthy plants without greatly increasing the top size over root size. The plants are checked regularly for insects, but few problems have occurred that have required the use of insecticides. Hand watering is sometimes necessary because of the differences in water requirements among the species in the lathhouse.

The plants remain in the lathhouse through the summer, fall, and most of the winter. In January or early February, the gallon cans are taken outside the lathhouse and placed in beds under overhead sprinklers.

Tarpaper pots are bound into bundles of 10 using a wrapper of tarpaper under the pots. The bundle is held together with 1/2-inch plastic banding or strapping held together at the ends with a strapping seal. These bundles can be moved around the lathhouse or loaded for shipping without damage to the pots to the plants themselves. The bundles of tarpaper pots are taken outside under overhead sprinklers and placed in the beds similar to those holding the gallon cans.

These beds are made by first laying down a 4- or 6-mil sheet of black polyethylene film 4 feet wide by 50 feet long. Next, a 4-foot-wide section of snow fence is rolled out over the top of the plastic film. Gallon cans are set directly on the snow fence. The spaces between the slats allow for good drainage under the cans. This airspace stops roots from moving out of the can through the drain holes in the bottom. The polyethylene film keeps weeds and grasses from growing in the beds.

Boards are placed along the edges of the beds which will hold the bundles of tarpaper pots. This helps reduce the drying of the outside pots along the edges of the beds.

The plants in these beds break dormancy and resume growth in the spring under full sunlight, thus eliminating the sunscald and wilting problems encountered when plants are moved from the lathhouse into full sunlight during the summer. These plants are now ready for field planting and further testing.

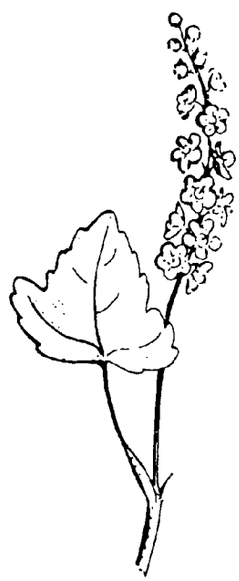
Vegetative propagation in the greenhouse

Small numbers of plants are propagated by cuttings to establish enough material for initial testing or to develop clonal material to start a seed nursery. Often it is desirable to isolate certain plants of an accession for seed production without destroying the other plants of the same accession in an adjacent planting.

Cuttings of hard-to-root woody plants are generally potted in 2 1/2- by 2 1/2- by 9-inch tarpaper pots. The pots are placed in a sweatbox with bottom heat and hand watered to keep the humidity at a high level. When cuttings are grown during the winter months, fluorescent lights provide a constant 13-hour-day length.

Plants are held in the greenhouse until danger of the last spring freeze is past. They are then taken to the lathhouse or lined out in the field for increased growth and observation--the same as is done with other plant materials.

The Soil Conservation Service does not now undertake large-scale production of any plant material. Only material for testing is produced. Once tested, the right species for a particular site or use, or the best variety in a group of varieties, commercial production is expected. Clones, seed from tested orchard material, or other propagating parts are supplied to cooperating nurserymen along with pertinent information about their culture. This is the reason for the lack of evidence of highly mechanized and streamlined production techniques that would be needed in a commercial operation.



Shrub establishment on game ranges in the Northwestern United States

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That area from the southern Rocky Mountains on the east to the crest of the Sierra Nevada on the west, and from southeastern Oregon, southern Idaho, and southwestern Wyoming southward through Utah and Nevada is often referred to as the Intermountain West. This vast expanse, and its extremes of climate, topography, and plant cover, provides habitats for a wide variety of wildlife species. Among them are the ungulate big game--deer, elk, pronghorn antelope, and bighorn sheep.

Big game habitats in the West are often conveniently classified as summer or winter ranges on the basis of elevational zonation or seasonal occupancy. Although not without exception (Adams 1959; Julander and others 1961), it is the wintering areas, by virtue of their restricted size and location, that require priority attention. Many of these winter habitats are in poor condition and are declining in both acreage and productivity (Klemmedson 1967). Efficiently and effectively improving the quality of these diminishing habitats is a major challenge.

One means of maintaining and improving habitat is through artificial measures--the direct establishment of food and cover plants. Seeding or planting shrubs and other forages often is the only practical means of restoring productive habitat where palatable food plants are lacking or sparse. In some areas, considerable effort has gone into the selection of adaptable species and the development of planting methods and equipment. This symposium provides an opportunity to summarize some of the problems, practices, and principles of establishing shrubs to improve big game ranges of the Intermountain West.

Intermountain environments

Intermountain climates are usually arid or semiarid. Only the sides and crest of the mountain ranges receive enough precipitation to support woodland or forest vegetation. Most of the big game wintering areas lie within the 5- to 25-inch rainfall belt. Hot, droughty summers, large diurnal temperature ranges, low relative and absolute humidities, general aridity, and wide yearly and seasonal fluctuations from mean values are characteristic climatic features (Wernstedt 1960).

Different parent materials and irregular landforms, plus the influence of climate and vegetation, have resulted in a multitude of soil types. Great soil groups range from the light-colored desertic soils of the arid zone to the dark-colored soils of the cool, subhumid and humid forested areas (Western States Land-Grant Universities and Colleges and U.S. Soil Conservation Service 1964). Shallow, stony, rocky, weakly-developed soils occur throughout the region. Zones of lime accumulation are typical. Saline and alkaline soils are widely distributed.

Plant cover in an area of such vast latitudinal and elevational gradients is extremely variable (Billings 1951). Vegetation types of the dry lowland steppe areas range from the southern desert shrub type (blackbrush *(Coleogyne ramosissima)* and creosote bush *(Larrea divaricata)*) through the salt desert shrub zone (black greasewood *(Sarcobatus vermiculatus)*, saltbushes *(Atriplex)*, and small bunchgrasses) to the northern desert shrub type (big sagebrush *(Artemisia tridentata)*, bluebunch wheatgrass *(Agropyron spicatum)*, and Idaho fescue *(Festuca idahoensis)*).

The many mountain ranges scattered across the region have resulted in a series of distinctive elevational belts of vegetation. The arrangement and composition of these zones in the eastern and western parts of the region differ. The montane zonal series on the east slope of the Sierras includes (as elevation increases): the pine-fir zone *(Pinus jeffreyi, P. ponderosa, P. lambertiana, Abies concolor)*, red fir zone *(A. magnifica)*, lodgepole pine-mountain hemlock zone *(P. contorta, Tsuga mertensiana)*, the white-bark pine zone *(P. albicaulis)*, and the sierran alpine tundra zone. Equivalent zones of the eastern Great Basin and the western slope of the Rockies include the juniper-pinyon woodland forest *(Juniperus osteosperma, J. scopulorum, Pinus edulis, Ephedra viridis, Artemisia tridentata, Purshia tridentata)*, mountain brush-ponderosa pine *(Quercus gambelii, Acer grandidentatum, Prunus virginiana, Amelanchier)*, aspen-fir *(Populus tremuloides, Abies concolor, Pseudotsuga menziesii, Symphoricarpos)*, spruce-fir *(Picea engelmannii, Abies lasiocarpa)*, and alpine tundra.

The juniper-pinyon, mountain brush-ponderosa pine, northern desert shrub, salt desert shrub, and southern desert shrub zones are particularly important to wintering big game.

Mention should also be made of the invasion of European annual grasses into the herbaceous understory. The principal invader has been cheatgrass *(Bromus tectorum)*, but medusahead *(Taeniatherum caputmedusae)*, foxtail chess *(B. rubens)*, and ripgut grass *(B. rigidus)* are common in certain types of habitats. Both cheatgrass and foxtail chess are widespread in the West, and medusahead continues to spread throughout the Intermountain area. Where conditions are favorable, these annuals have significant competitive ability and often dominate the understory if perennial vegetation is disturbed.

Environmental hazards to direct establishment

Disturbed sites on big game winter ranges of the Intermountain West present variable and often difficult environments in which to reestablish desirable shrubs. Of the many factors that influence direct establishment, two sets of variables are particularly formidable: (1) the conditions characteristically associated with an arid environment, and (2) the damaging impacts of biotic agents--large herbivores, rodents, lagomorphs, insects, and disease.

Many environmental problems stem from the absence of rainfall during much or all of the summer season, high daytime temperatures, and low relative humidities. High evaporation and transpiration rates result in a rapid loss of soil moisture. In such conditions, competition between newly emerged seedlings and established vegetation is severe (Schultz and others 1955; Rickard 1967; Cable 1969). Ineffective control of competing species is a major obstacle to seedling establishment (Hormay 1943; Holmgren 1956; Hubbard 1957).

High soil and air temperatures can adversely affect seedling survival and growth. Hubbard (1964) reported observing bitterbrush seedling losses that he attributed to excessive soil surface temperatures. Soil surface temperatures in southern Idaho commonly reach 140° to 150° F. and a high of 168° F. has been recorded (Ferguson 1972). Sosebee and Herbel (1969) noted reduced emergence, survival, and shoot growth of several range plants grown under high soil temperature regimes.

Destruction or damage by animals constitutes a hazard to artificial regeneration (the seeding or planting) of shrubs. Small mammals, particularly rodents, are destructive to both seed and seedlings. Seed-eating rodents can consume large quantities of seed and contribute importantly to seeding failures (Holmgren and Basile 1959). Casebeer (1954) reported that rodents disturbed 98 to 99 percent of seed spots planted with untreated bitterbrush seed. Brown and Martinsen (1959) suggested that rodents caused more failures in early seeding programs than any other single factor. The size and composition of rodent populations fluctuate widely and may greatly alter the amount of seed destruction from one year to another. Mice (principally *Peromyscus* and *Microtus*), chipmunks *(Eutamias)*, and ground squirrels *(Citellus)* are probably most responsible for seed losses in the Intermountain region.

Clipping, girdling, and browsing damage to seedlings and young plants is another major concern (Holmgren and Basile 1959; Hubbard and McKeever 1961; Ferguson 1968; Plummer and others 1968). Clipping by rodents and rabbits often causes high rates of seedling mortality. In some areas, destructive use by rabbits is a significant problem (Hubbard 1964). Root injury or root cutting can occur on both seedlings and well-established plants as a result of pocket gopher and mouse activity. Severe browsing by big game or livestock can kill seedlings outright or weaken them to the point of eventual death.

Insects pose an additional biotic threat. Grasshoppers *(Melanoplus)*, the Great Basin tent caterpillar *(Malacosoma fragilis)*, cutworms *(Lycophotia)*, and wireworms *(Elatridae)* injure or destroy bitterbrush seedlings (Holmgren 1954; Hubbard 1956a; Clark 1956). Other insects either suspected or known to be injurious to bitterbrush have been reported by Ferguson and others (1963), Basile and Ferguson (1964), Nord (1965), and Johnson and Ross (1967). Larvae of the geometrid *(Anacamptodes clivinaria profanata)* are destructive to curlleaf mountain mahogany *(Cercocarpus ledifolius)* in southern Idaho (Furniss and Barr 1967; Scheldt and Tisdale 1970). The sagebrush defoliator *(Aroga websteri)* infests big sagebrush and other shrubs throughout the Intermountain region (Hall 1965).

Other hazards to direct establishment of shrubs include trampling by hoofed mammals (Holmgren and Basile 1959), frost heaving (Biswell and others 1953; Hubbard 1964), frost injury (Smith and others 1965; Stickney 1965), and disease organisms, particularly damping-off fungi (Holmgren 1956; Nord 1965).

Problems and progress

Some of the major procedural problems of range revegetation include (1) evaluation of a site's suitability and need for revegetation, (2) identification of species and varieties that establish readily and yield herbage of satisfactory volume and quality over a long period, (3) preparation of a site for revegetation, (4) assurance of good quality seed or planting stock, (5) application of satisfactory planting techniques, and (6) management of established stands for maximum, dependable production (Subcommittee on Range Research Methods of the Agricultural Board 1962). These broad problem areas are directly applicable to artificial establishment of shrubs on game ranges and provide convenient points of reference.

Site evaluation

Establishment of shrubs, even on good sites, is often difficult and costly. Planting emphasis may be placed only on better soils and sites to justify high investment costs (Brown and Martinsen 1959). Frequently, however, the sites most in need of improvement are the poorest. While the deep, fertile soils associated with gentle topography may be most productive, it is usually the shallow, rocky soils of steep south-facing exposures that must be restored for improved soil stability and forage production.

Guidelines for choosing among sites for planting programs, even though the range of choice is often limited, are presently far from adequate. Some work in this direction has begun in Utah where Plummer and others (1970a) are investigating the possibility of using indicator plants to predict site productivity. Much needs to be learned about recognizing suitable planting sites and site potentials for shrub species.

Planting site decisions must take into account both feasibility and need. If some desirable species remain on poor-condition winter ranges, alternative strategies to artificial revegetation may be available. In some cases, reduction of big game browsing pressure or judicious manipulation of livestock use (Hormay 1970) may permit native shrubs to increase at only a fraction of the cost of revegetation. Top-pruning to increase the shoot growth of decadent plants has been successful for some species (Ferguson and Basile 1966; Thompson 1970). Controlled burning is an applicable treatment in some cover types (McCulloch 1969; Aro 1971). In other areas, unstable soils or high big game populations (and resultant trampling and browsing damage) may preclude effective artificial revegetation.

Species adaptability

Adaptability implies that a species has the ability to establish and maintain itself in a selected environment. Accordingly, a first consideration in choosing a species for artificial revegetation is its ability to survive, grow, and reproduce on the planting site. Shrubs planted for forage must also be capable of producing substantial amounts of herbage available for consumption. Other species characteristics influence the selection of a shrub for a particular site or purpose. These may include growth rate, growth form, longevity, competitive ability, drought resistance, browsing tolerance, reproductive capacity, nutritional value, palatability, and relative susceptibility to damage by animals or disease. Multipurpose or nonconsumptive uses may be additional considerations (e.g., the value of the species as a food or cover plant for cohabiting animals or characteristics of growth form particularly suited for stabilizing soils). A dependable seed supply that can be harvested, cleaned, and handled is an important economic consideration (Holmgren and Basile 1959).

Species lists and adaptability evaluations of shrubs for extensive planting on winter game ranges of the Intermountain region are becoming increasingly available. Much of the work on shrub adaptability has been done in Utah where Plummer and others (1970a) have assembled tentative adaptability ratings for 121 shrubs and trees. Each species is assigned a numerical rating based on the shrub's range of adaptability to various planting sites. Papers listing shrub species adapted for planting in other Intermountain areas have been published by Holmgren (1954), Plummer and others (1955), Brown and Martinsen (1959), Hubbard (1964), and Hull and Holmgren (1964).

Recent research (Plummer and others 1970a) is demonstrating that the species alone is no longer an adequate basis for finding adapted shrubs for revegetation. Wide differences in adaptability, growth, and palatability exist between ecotypes of single shrub species. As more ecotypes are recognized and tested and new strains are developed, continuing work on adaptation to site and use will be required.

Site preparation

Site preparation removes or reduces established plants that compete with a planted species and prepares the soil surface for planting. Harsh environments and competing vegetation make initial establishment of some shrubs difficult. Once established, shrubs generally grow, but initial establishment problems can be formidable, particularly for bitterbrush, serviceberry, mountain mahogany, and other slow-developing species. The mortality rate among newly planted or emergent seedlings is high on unprepared areas during the summer drought period.

Topography, soils, and existing plant cover govern the tools and methods used to reduce competing vegetation. Specialized equipment adapted to rangeland conditions has been developed (U.S. Forest Service 1957). On level or moderately sloping terrain, tractor-drawn tillage implements, such as the brushland plow (Hubbard 1964), the double-wing moldboard plow (Holmgren and Basile 1959), pipe harrows, undercutters (Plummer and others 1968), and tractor-drawn blades (Brown and Martinsen 1959) have been used. Modified shovels are used for hand scalping areas too steep or rocky for mechanized equipment (Holmgren and Basile 1959).

Bulldozing and chaining or cabling are mechanical treatments used to reduce competition from juniper, pinyon, and other conifers (Plummer and others 1968; Aro 1971). For anchor chaining, the most commonly used method, the ends of a chain, 250 to 600 ft. long and made up of links weighing 25 to 90 lb., are attached to two crawler tractors which drag the loop of chain through the trees to knock them down or rip them out. Double chaining, the same process repeated in the opposite direction, also provides a covering for seed sown prior to the second chaining. Welding 18- to 20-inch lengths of rail to the links increases efficiency. Chaining is adapted to variable topography and is particularly useful on moderately steep and rocky areas.

Controlled burning and chemical treatments can also be effective methods for reducing competition (Brown and Martinsen 1959; Plummer and others 1968; Aro 1971).

Seed quality

Obtaining adequate supplies of good quality shrub seed is a continual problem in game range restoration programs. Shrub seed generally must be harvested from native stands on wildland areas since the needed species are seldom grown for commercial seed production. Consequently, shrub seed can be expensive, occasionally of poor quality (Ferguson 1967), or from strains unsuited for specific planting sites. Also, native stands of shrubs produce seed irregularly and production can vary according to the species, site, season, and diversity of soil and climate (Nord 1963).

There is a need for cultural programs that can consistently provide quality seed at a reasonable cost. As superior ecotypes are found or developed, seed propagation will become increasingly important. To this end, some lands in Utah are being planted with shrubs for future seed production purposes (Plummer and others 1970a). Also being studied is the question of how to grow quality seed in quantity for several native species. Private landowners are encouraged to produce shrub seed for which there is a profitable market.

Mechanical means of harvesting seeds from wildland stands are in the preliminary stages of development. For example, a prototype vacuum harvester is being perfected by the U.S. Forest Service Equipment Development Laboratory (Nord 1963; Plummer and others 1970a).

Planting procedures

There are three general direct seeding methods: (1) Spot seeding (sowing in prepared spots), (2) drill seeding, and (3) broadcast seeding (either from the air or the ground). Choice of method may vary with planting objectives, size of planted area, terrain, competing vegetation, soils, species mixtures, and economic constraints. Each method has its particular advantages and disadvantages.

Topography too steep for heavy machinery requires spot seeding by hand methods. On such areas, specially designed hand planters can be used to gage the number and the depth at which seeds are planted. The planters are easily modified to accommodate different seed sizes and different planting depth requirements.

Several types of heavy-duty seed drills can be used to sow shrub seed. The rangeland drill has been used successfully throughout the Intermountain area (Hubbard 1964). Drills provided with moldboard plows that combine site preparation and seeding operations have been used extensively in Utah (Plummer and others 1968) and Idaho (Holmgren and Basile 1959). Drill seeding is faster and cheaper than spot seeding, but is not well adapted for use on steep slopes or areas covered with rocks or debris.

"Seed dribblers," which drop seed into the cleatmarks left by crawler tractor treads, have proved to be useful in some areas (Plummer and others 1968).

Both fixed-wing and helicopter aircraft are used to broadcast seed large areas on which previous site preparation treatments have been completed. Helicopters are more versatile for seeding small, scattered, and irregular tracts.

On the droughty sites of the Intermountain region, shrub seed normally needs to be covered--regardless of the seeding method employed (Hubbard 1956b; Basile and Holmgren 1957). Broadcast seed is generally covered by pipe harrowing or by chaining the area after sowing.

Seeding rates depend on a number of variables, such as species planted, seed quality, establishment vigor, growth characteristics of the species, native competition, condition of the seedbed, and method of seeding. Some variables can be assessed with reasonable accuracy; others must be estimated from past performance or published guidelines. At best, seeding rates are only rough guides since environments vary from place to place and from year to year. Drill seeding requires more seed than spot seeding, but less than broadcast sowing. It is not generally good practice to economize by reducing the amount of seed sown. Seed costs are often only a small part of the total cost of revegetation.

Holmgren and Basile (1959) recommended planting six to eight bitterbrush seeds at each of three spots on hand-prepared scalps. More than one seedling usually emerges from each seed spot and establishment success improves as the number of emergent seedlings increases (Ferguson and Basile 1967).

Drilling rates of 1-1/2 to 2-1/2 lb. of bitterbrush seed and 6 to 8 lb. of grass seed per acre are suggested for seeding bitterbrush-grass mixtures on southern Idaho game ranges (Holmgren and Basile 1959). In California, 3 lb. of viable bitterbrush seed per acre has usually been satisfactory for drill seeding sites receiving 12 inches or more of precipitation (Hubbard 1964). Eight to 10 lb. per acre of a seed mixture (shrubs forbs, and grasses) is recommended for drill planting in Utah and 12 to 20 lb. for broadcast seeding (Plummer and others 1968).

For the Intermountain region as a whole, seeding in the fall or winter has been most effective. However, Hubbard (1964) found spring seeding best in California, provided that soils were sandy loams or heavier and that annual precipitation exceeded 12 inches and was well distributed in the spring. Spring seeding was not recommended for dry sites that have but a brief period of adequate soil moisture.

Direct seeding in late fall and early winter has resulted in good establishment of most shrub species in Utah (Plummer and others 1968). Holmgren and Basile (1959) recommended seeding bitterbrush and grass mixtures in October and November in southwestern Idaho and in October farther east.

Transplanting, which may be a better method of establishing shrubs on particularly severe sites, normally is most successful when completed as early in the spring as conditions permit. Transplanted shrubs need as much time as possible to reestablish functional root systems before soil moisture declines to critically low levels.

Managing newly established stands

Development and permanence of shrub stands, once established, depend on the control of potentially damaging factors. Fires, insects, rodents, rabbits, game, livestock, and perhaps other factors, singly or collectively, can impair the development of or destroy shrub plantings. Proper care and protection can reduce the adverse effect of some of these factors.

Livestock grazing of newly revegetated areas should be prohibited until plants are firmly established and productive. Liberal harvest programs can reduce damaging big game impacts. Although survival and growth are reduced by moderate browsing or trampling by big game, the success of some shrub plantings may not be seriously jeopardized (Ferguson 1968). However, persistent heavy browsing retards the growth of newly established shrubs (Dealy 1970) and can threaten their continued existence. Overbrowsing by game can be partly avoided if planted areas are large enough to prevent damaging concentrations.

In some areas, rabbits are more harmful than big game or livestock (Hubbard 1964; Plummer and others 1968). Rodents and insects can also be seriously destructive (Holmgren and Basile 1959). Suggested methods of control or partial control of these animals are available (Subcommittee on Insect Pests 1969; Subcommittee on Vertebrate Pests 1970).

Status of game range improvement

Compared to the need, research on methods of improving game ranges through artificial means is meager, but such studies have provided substantial progress toward solution of major problems and developed inceptive patterns of application. Several "how to" publications recommend plant species and procedures for improving game ranges in the Intermountain West. Chief among these are reports by Holmgren and Basile (1959) for southern Idaho, Hubbard (1964) for eastern California, and Plummer and others (1968) for Utah. Work done beyond the arbitrary boundaries of the Intermountain region is also applicable (Brown and Martinsen (1959) in Washington, and Springfield (1970) in New Mexico and Arizona).

Though limited and provisional in some areas, advances are being made in operational programs. Nearly 10,000 acres have been improved for wintering big game in Nevada;[1] almost 15,000 acres in southern Idaho;[2] and over 75,000 acres in Oregon.[3] Operational projects have progressed most rapidly in Utah where over 120,000 acres have been treated (Plummer and others 1970b). Most of the Utah work has been done in the juniper-pinyon type, a type occupying almost 60 million acres in the Western United States (U.S. Forest Service 1958). Although summary statements are unavailable, wildland ranges in Colorado and California are also being improved specifically for the benefit of big game.

A representative example of deer range improvement in Utah is a 1,000-acre restoration project in an area that formerly supported about 400 juniper and pinyon trees per acre. In November 1961, the site was chained in one direction, aerially seeded at a rate of 12 lb. per acre using a mixture of nine species, and then chained a second time. The second chaining covered the seed and removed trees that had not been killed by the first chaining. Additional hand seeding of shrubs was done on selected sites within the project area. Before treatment, the area provided about 70 lb. of understory herbs

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[1]Personal correspondence with M. A. McColm, Nevada Department of Fish and Game, Elko, Nevada.

[2]Personal communication with L. L. Mohler, Idaho Fish and Game Department, Boise, Idaho.

[3]Personal communication with R. U. Mace, Oregon State Game Commission, Portland, Oregon.

Table 1.--*Herbage production (field weight, lb/acre) and percent ground cover by vegetal classes in 4 selected years on range seeded in November 1961 (adapted from Plummer and others 1970b)*

Plant type	Herbage production				Ground cover			
	1964	1966	1967	1969	1964	1966	1967	1969
Seeded grass	1,097	449	552	1,124	35.0	22.0	39.3	40.0
Native grass (perennial)	142	2	71	1	4.8	.5	2.7	.7
Annual grass (mostly cheatgrass brome)	56	1	5	0	12.0	0	.1	0
Seeded forbs (mostly alfalfa)	179	136	259	429	3.7	4.4	10.3	12.8
Perennial forbs	45	5	14	5	.9	.1	.1	.2
Annual forbs	8	0	6	0	0	0	0	0
Shrubs	50	88	65	147	1.4	.8	2.1	2.7
Total production and cover (exclusive of trees)	1,577	681	972	1,706	57.8	27.8	54.6	56.4
Trees	318	483	388	1,030	4.5	4.2	4.5	6.0
Litter					26.5	55.4	28.0	23.3
Total vegetal cover					88.8	87.4	87.1	85.7
Bare ground					11.2	12.6	12.9	14.3
Precipitation (inches)	14.30	9.83	14.01	14.84				

per acre. In 1964, 3 years after treatment, the site produced nearly 1,600 lb. of total herbage per acre and by 1969, over 1,700 lb. per acre (table 1). Shrub yields increased from 50 to almost 150 lb. per acre over the same period. As a class, the shrubs grew more slowly than the herbaceous components, but their productivity undoubtedly will continue to increase as they mature.

Another example illustrated the degree of improvement that can be achieved from artificial improvement measures. A 10-year-old bitterbrush seeding on a deer winter range near Boise, Idaho, produced over 620 lb. of ovendry annual twig growth per acre during the 1967 growing season. Stand density was about 760 bitterbrush shrubs per acre.[4]

These examples, as well as those of other States, show that substantial improvement of big game winter range can result from artificial establishment of shrubs and herbs. Many thousands of acres in the Intermountain West have a potential for similar improvement.

[4]D. E. Medin, and R. B. Ferguson. Unpublished data on file at Intermountain Forest and Range Experiment Station, Boise, Idaho.

Summary and conclusions

Improvement of Intermountain big game ranges by seeding and planting shrubs is a product of studies largely conducted during the last two decades. Investigations have been focused on five general problem areas, namely, the determination of adapted species, methods of removing competing vegetation, optimum planting seasons and rates, satisfactory planting procedures, and methods of protecting seeds and seedlings from biotic agents. This investigative approach has required trials of plant species and planting techniques in experimental areas, outplantings to determine the ability of potentially useful species to survive and grow on a variety of sites, and pilot plantings to test methods and costs.

From these studies, several basic principles for successful planting of wildland ranges have been developed (Plummer and others 1968): (1) Proposed changes in plant cover must be determined to be necessary and desirable, (2) terrain and soil type must be suited to the change selected, (3) precipitation must be adequate to assure establishment and survival of planted species, (4) competition must be low enough to assure establishment of desired species, (5) only species and strains adapted to the area should be planted, (6) mixtures of species (rather than a single species) should be planted, (7) sufficient seed of acceptable purity and viability should be planted to assure a stand, (8) seed must be adequately covered, (9) planting should be done in the season of optimum conditions for establishment, and (10) the planted area must be suitably protected.

Accomplishments throughout the Intermountain West illustrate the progress that has been made in developing the principles and procedures required to establish shrubs and herbs in the difficult environments of big game winter ranges. Current results also demonstrate that effective planting depends on the judicious application of existing skill and information and that new knowledge must be developed through research and experience.

Major opportunities exist for improvement. Additional work should be directed toward:

1. More precise determination of the adaptability of shrub species and ecotypes to particular environments. Studies of site requirements and physiological tolerances are especially needed.

2. Development of new strains by selection and breeding. Improvement of shrub quality, establishment characteristics, and growth by means of selection and artificial hybridization is a potentially productive area of investigation.

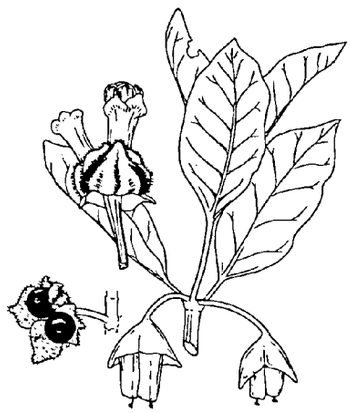
3. Expansion of the cultural knowledge required to grow shrubs. Conditions most favorable for germination, treatment of seeds to break dormancy and facilitate maximum germination, optimum seeding dates, and seeding depths have been determined for relatively few shrub species. For nursery-grown transplant stock, information is needed on desirable seedling density in nursery beds, practicality of seedbed fertilization, appropriate timing and amount of irrigation, value of root pruning, timing of lifting operations, and suitable storage conditions following lifting. Additional investigation of procedures for growing and planting shrub seedlings in containers is needed. For example, planting shrub seedlings grown in "planting bullets" (Walters 1968) is now being evaluated on several southern Idaho sites.

4. Development of dependable supplies of quality seed. Procurement of good seed in adequate quantities, at a reasonable cost, continues to be an obstacle to large-scale seeding.

5. Recognition of suitable planting sites and site potentials. Guidelines for choosing areas to be revegetated must be improved from field experience and further research.

6. More effective methods and more efficient equipment for removing competing vegetation, preparing planting sites, sowing seed, and planting seedlings. Site preparation methods for steep slopes are still crude and costly.

7. Protection of seeds and seedlings from the damaging effects of biological agents. Destruction by rodents, rabbits, and insects remains a critical problem. Our skills in this area are far from adequate and recent governmental restrictions on the use of pesticides have intensified the difficulties.



Using mechanical equipment to modify the seedling environment[1]

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In arid and semiarid zones, the soil surface is infrequently moistened and the evaporation rate is high. Establishing seedlings is often difficult because of an adverse microenvironment (rapid drying, unfavorable temperatures, and crusting of the soil surface). Accordingly, the primary objective of seeding procedures is to place the seed in a favorable environment for germination and establishment of the seedling. This often requires varying the procedure to fit the site.

Good seedbed preparation for range seeding in some areas involves retaining a firm seedbed that favors infiltration and storage of moisture and leaving a trash-covered surface (Pearse 1952). Shallow disking, or other treatment that reduces weed competition, generally accomplishes these objectives. More intensive tillage is usually avoided not only because of increased cost but also because of the problem of excessive disturbance of the soil surface, bringing up heavier subsoils, or burying the friable topsoil and litter. Wind erosion is often a problem on loose, unprotected seedbeds. Loose seedbeds should be allowed to settle or be otherwise compacted before seeding.

In this paper, press wheel is used to describe soil firming prior to seeding, and packer wheel is used to describe soil firming after seeding. A scalper blade is a sweep that removes debris and plant competition from a seeded row. Ripping is used to describe a method of fracturing a hardpan, plowpan, or other impenetrable layer that impedes infiltration of moisture. Pits are shallow indentations or basins made in the surface of the soil to retain water from rainfall or snowmelt on a site.

Ripping, pitting, and furrowing

Water conservation in site preparation is essential in arid and semiarid areas. Staggered pits or interrupted contour furrows increase soil moisture (Anderson and Swanson 1948). They may be constructed with eccentric or cutaway disks.

The author has conducted pitting and furrowing trials on the Jornada Experimental Range near Las Cruces, New Mexico. A loam site was treated with a pitter disk seeder. The maximum summer soil temperatures at the 1.3-cm. depth were 10° C. lower (41° vs. 51° C.) in the pits than on adjacent flat areas. There was 10.5 cm. rainfall during the 66 days in summer following treatment. The soil moisture potential at the 1.3-cm. depth

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[1]Cooperative investigations of Plant Science Research Division, Agricultural Research Service, U. S. Department of Agriculture; and the Agricultural Experiment Station, New Mexico State University, Las Cruces, New Mexico. Journal article 389, New Mexico Agricultural Experiment Station.

was between 0 and -15 bars for 36 days in the pits but none was recorded on the flat area. Figures 1 and 2 show the daily rainfall and soil moisture potential at the 1:3- and 10.2-cm. depth for the 66-day summer period. A fair stand of grasses emerged on the pitted area in September (Herbel 1972). Subsequent seedings with the pitter disk have been failures, probably because of poor seed placement. The seed is placed on the surface of the soil and covered with a drag chain.

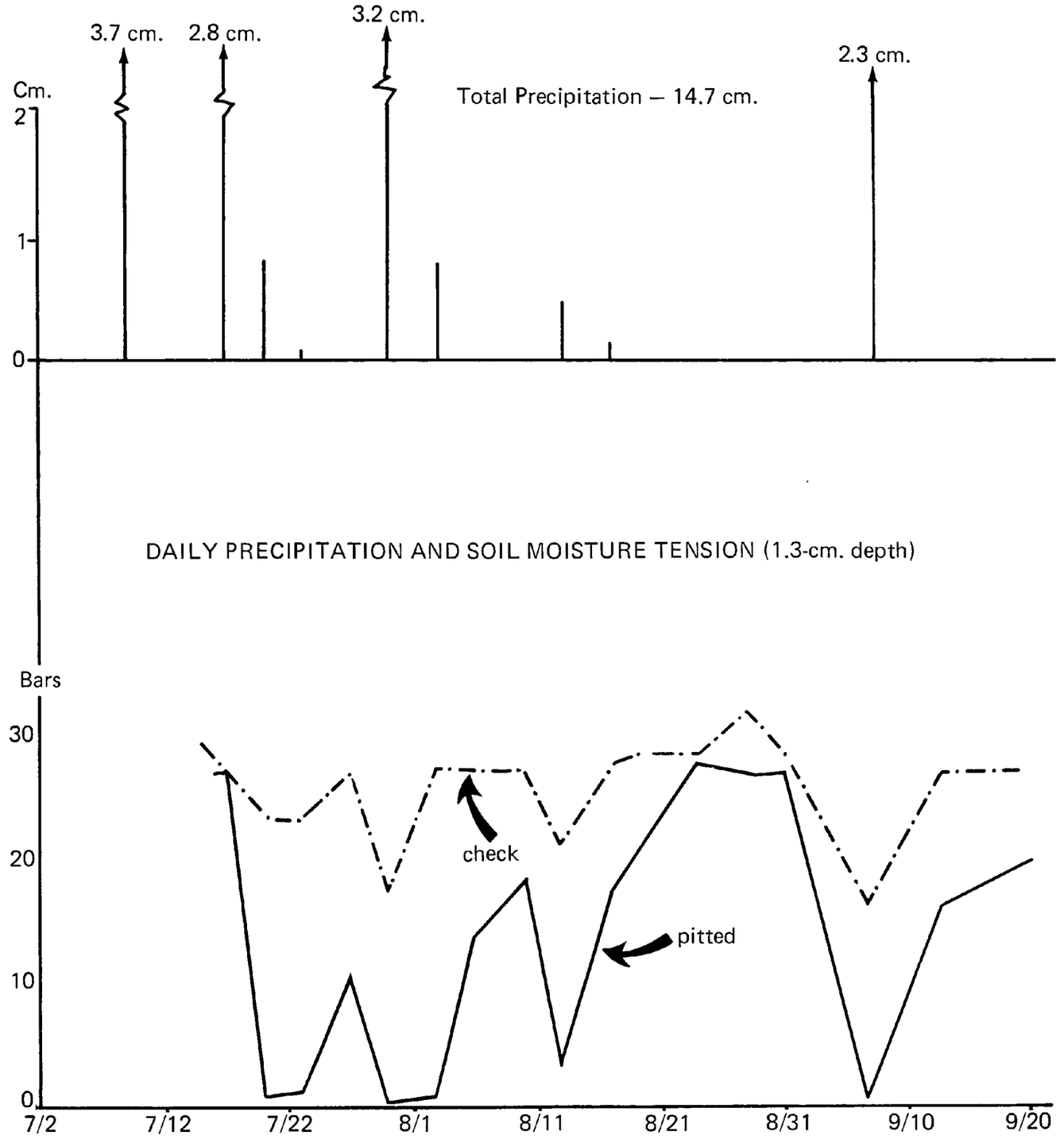

Figure 1.--Daily precipitation (cm.) and soil moisture potential (bars) at the 1.3-cm. depth in the bottom of pits and an adjacent flat area on the Jornada Experimental Range (Herbel 1972). The pits were formed with a pitter disk on July 11, 1962. Soil moisture was recorded twice weekly during the period July 16-September 20.

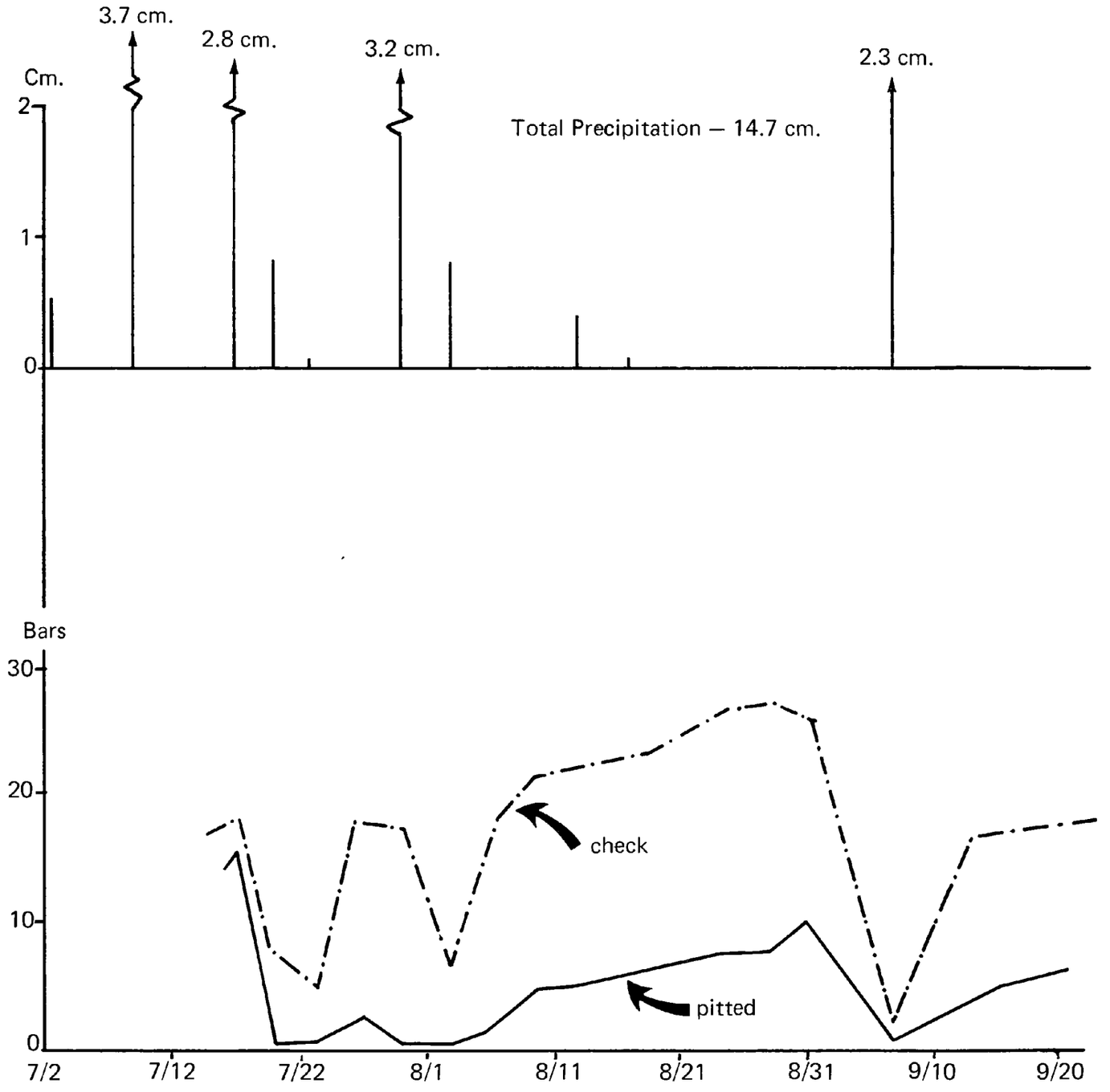

Figure 2.--Daily precipitation (cm.) and soil moisture potential (bars) at the 10.2-cm. depth for the same treatment as figure 1.

North-south and east-west furrows, 30 cm. deep, were established by the author on a loamy fine sand site in early summer. Grasses were seeded on the middle of each slope and in the bottom of each furrow. Excellent emergence was obtained on all the slopes within a few days after seeding. The average maximum air temperature 10 cm. above the surface of the ground during the summer was 34° C. The average maximum

temperatures at the 1.3-cm. depth were 43°, 44°, 48°, and 43° C. for the north-, east-, south-, and west-facing slopes, respectively. During a 66-day period during summer, 11.7 cm. rainfall was recorded. Moisture potential at the 1.3-cm. depth was between 0 and -1 bar for 4 days on the slopes of the furrows and 13 days in the bottoms of the furrows (fig. 3). Deposition of sand in the furrows was a problem (Herbel 1972).

Pitting followed by cultipacker-seeding was the most consistent method of successfully seeding ranges in Arizona (Anderson and others 1957). Ripping and contour furrowing were also good methods of seedbed preparation on fine-textured bottomland soils.

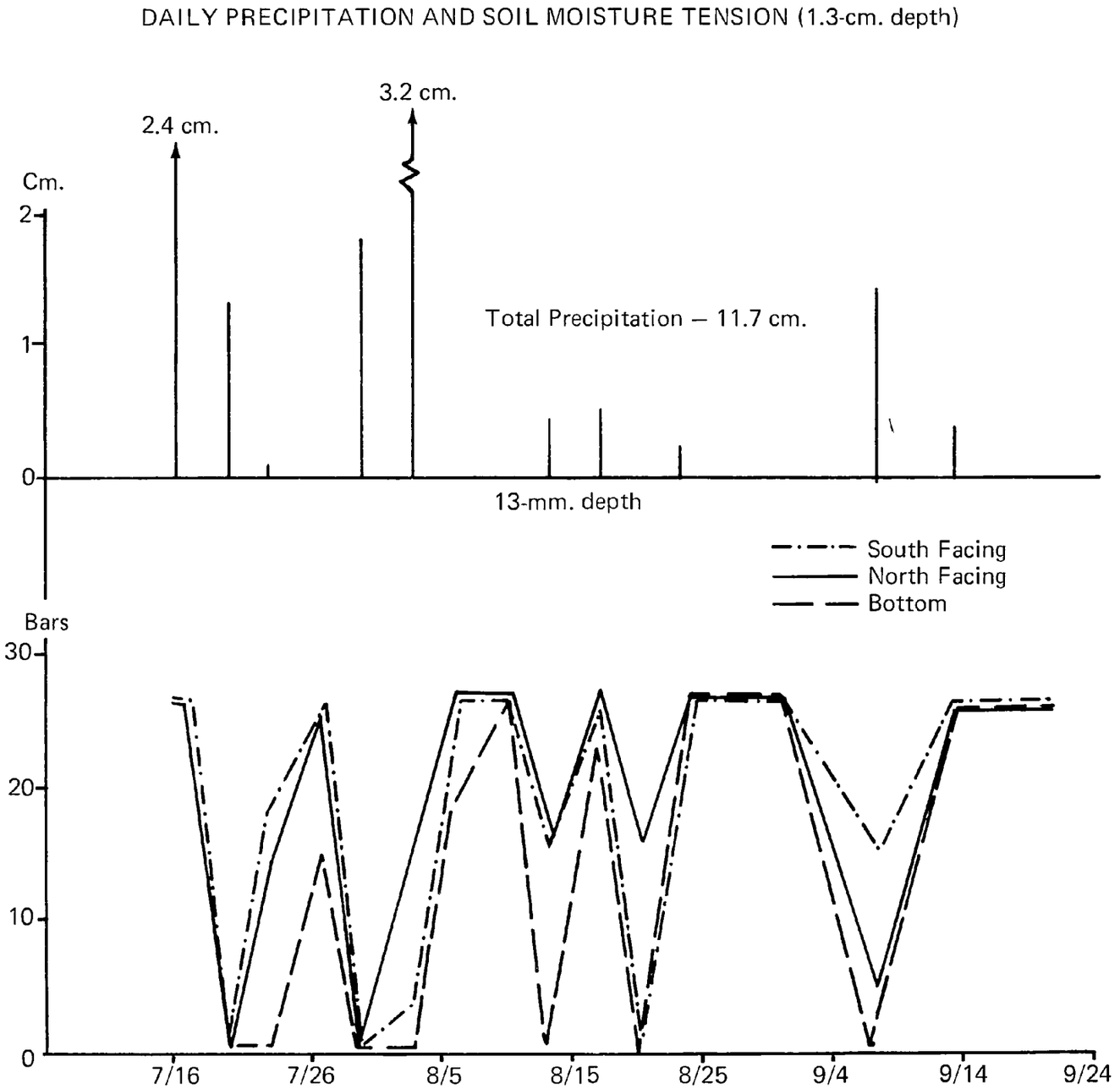

Figure 3.--Daily precipitation (cm.) and soil moisture potential (bars) at the 1.3-cm. depth in the bottom of a furrow and the middle of the north- and south-facing slopes of a furrow on the Jornada Experimental Range (Herbel 1972). The furrows were formed on July 11, 1962. Soil moisture was recorded twice weekly during the period July 16-September 20.

Ripping decreased runoff and erosion in New Mexico, but seeding attempts were mostly unsuccessful (Dortignac and Hickey 1963).

Range seeding with several grass species was studied near Barnhart, Texas, during 1950-55 (Thomas and Young 1956). During this period of below-average precipitation, most seedings were unsuccessful except those made in conjunction with pitting in 1954. Ten percent of the pits on open upland soils had established seedlings with broadcast seeding following pitting. Only 4.7 percent of the pits had seedlings when the seed was broadcast in front of the pitter.

In a 1958 trial at Bushland, Texas, seeding in the bottom of pits and broadcast seeding following furrowing to a 15-cm. depth were both failures (Dudley and Hudspeth 1964).

Three seeding methods in conjunction with disk pitting were studied in Oklahoma (Whitney and others 1967). Precision drilling of seeds across the length of the pits was generally superior to broadcasting seed into grooves followed by drag chains or broadcasting seed followed by a packer wheel. The drilling was accomplished by using opener blades which made slits for the seed 0.6 cm. wide and 1.9 cm. deep. A packer wheel followed to close each slit and to pack soil over the seed.

Pitting accompanied by seeding has been an unsuccessful practice for seedling establishment in the northern Great Plains (Barnes and others 1958). There was too much competition from native plants remaining after pitting during dry periods in the summer.

Successful regeneration of rangelands in the Northeast Pastoral Zone of South Australia depends on (1) trapping windborne seed, (2) concentrating moisture from light rains, and (3) protecting young seedlings from the effect of blasting by windborne sand (Young 1969). Contour furrows and pits successfully accomplished this, but it is difficult to keep furrows exactly on the contour. A tined pitter was developed, and it has resulted in a natural revegetation of desirable plants such as bluebushes (*Kochia* sp.) and saltbushes (*Atriplex* sp.). The tined pitter is mounted on two wheels with offcenter axles. As the pitter wheels turn, the sweeps are raised and lowered, thus forming interrupted pits. Two of the three sweeps are fastened to the front of the framework, and the other is fastened on the rear part of the framework. All the sweeps are in the ground together, but staggered pits are achieved because one sweep is mounted behind the other two. The pits are 60-90 cm. long, 15-25 cm. wide, and 10-15 cm. deep. The pit has sloping sides and ends, and the displaced earth is deposited on either side of the pit.

Frost and Hamilton (1965) have developed a basin-forming machine designed to produce fan-shaped basins on rough desert land. The fan-shaped basin has a steep sidewall (15-25 cm. deep) on the downslope side and gentle slopes to the bottom on the other three sides. A basin of this shape, sloping in three directions to one point, enables seed placement at various elevations to take advantage of various types of rainstorms. Grass stands have been established on both heavy- and light-textured soils near Tucson, Arizona, under various rainfall conditions.

The broad, shallow pits made with the basin-forming machine developed by Frost and Hamilton (1965) last longer than conventional pits in southern Arizona (Slayback and Cable 1970). Over a 4-year period, average production of seeded buffelgrass (*Cenchrus ciliaris*) was 773 kg./ha. on broad pits and 283 kg./ha. on conventional pits. The latter were made with a pitting disk. Initial establishment of buffelgrass was generally better in the conventional pits. However, production on the latter generally declined after the second year because of decreasing capacity of the pits to hold water. The broad pits were still effective, though partially filled, 5 years after construction.

The use of check dams or bulldozer pits has proven to be a successful method of establishing grasses, forbs, and shrubs on the Black Gap Wildlife Management Area in western Texas (Moore 1960). A series of pits are located on short or restricted watersheds or in overflow sites where soil is eroded. A dam 2.4 m. wide and 0.8 m. high is rapidly constructed. Seeds are hand-sown several weeks prior to the expected summer rains and covered immediately with a hand rake. The average annual precipitation at Black Gap is 18 cm.

Branson and others (1966) evaluated the effects of the following mechanical soil treatments on water storage: interrupted furrows made with a Model B Contour Furrower, broadbase furrows made with a motor grader, trenches made with a motor grader, pits made with spike-tooth or rotary pitters, pits made with an eccentric disk pitter, ripping with an auger ripper, and ripping with an auger ripper equipped with a furrow opener. The most effective treatments were contour-furrowing at intervals of 0.9-1.5 m. and depths of 20-25 cm. and broadbase furrows which had low dikes (0.5 m. high). The most consistent beneficial responses occurred on medium- to fine-textured soils.

Furrows 8, 15, and 30 cm. deep were spaced 1:8, 4.6, and 9.1 m. apart on a gently sloping sandplain in central Australia (Winkworth 1963). Surface flow water accumulated in the furrows during five rainy periods in 2 years. Spacing effects were inconclusive and greater accumulation in the deeper furrows was probably due to their larger and steeper banks. The moisture in the surface 2.5 cm. dried to -15 bar potential in about 1 day in the bottom of the furrows, as well as between the furrows. The 2.5- to 7.5-cm. layer remained moist 2 to 5 days following rain.

Hull (1970) studied the effects of eight furrow conditions on grass establishment in southeastern Idaho. Seedings in 2.5-, 5-, and 10-cm. furrows; north exposures; and on the level were superior to those on south exposures and on the ridges of furrows.

The inner coastal foothills in California have been successfully seeded by use of contour furrows (Cornelius and Burma 1970). Desert saltbush *(Atriplex polycarpa)* and several grasses are well adapted for seeding in that area.

Contour-furrowing and seeding with crested wheatgrass *(Agropyron desertorum)* were studied on saltsage rangeland in Wyoming (Nichols 1964). The major species on that area is Nuttall saltbush *(Atriplex nuttallii)*. The range was contour-furrowed and seeded in 1957. A combination furrowing and seeding machine made furrows approximately 1.5 m. apart and 25-30 cm. deep. A device created dams in the furrows every 3 m. After 4 years, the cover of Nuttall saltbush was similar on treated and untreated areas; the production of saltbush was 79 percent greater on the treated area (533 vs. 298 kg./ha.); and in addition, there were 539 kg./ha. of crested wheatgrass.

Closely spaced, interrupted, contour furrows are an effective reclamation treatment on eroded areas of the Cobar Peneplain and similar areas in western New South Wales in Australia (Cunningham 1967). The most suitable spacing between furrow lines was 1.2-1.5 m. That spacing was sufficient to moisten the furrows adequately and yet prevent runoff. The average annual precipitation is 30-38 cm. Ripping was ineffective because the rip lines sealed over within a year. Herbaceous plants and saltbushes (*Atriplex* sp.) from natural sources became established in the furrows.

An opposed disk plow with a centrally mounted ripper point was developed for furrow-seeding the Ord River Regeneration Project in northwestern Australia (Fitzgerald 1969). It is equipped with a seedbox and mounted on a three-point hookup on a wheel-type tractor. Early experience indicated that a bank formed from loose soil heaped onto compacted ground collapsed when wetted. The bank of loose soil proved more stable when a ripper point was placed between the disks. Buffelgrass, birdwoodgrass (*Cenchrus setigerus*), and kapokbush (*Aerva javanica*) have been successfully seeded with this technique.

Deep furrow drilling generally resulted in better revegetation than other methods on dry sites in the Intermountain region of the Western United States (Plummer and others 1955). McGinnies (1959) found that furrows only 10 cm. deep significantly increased available soil moisture and improved seedling establishment over an unfurrowed check. In unstable soils, the furrows were often filled by soil from local erosion in a relatively short time.

Waterponding

Waterponding assisted in reclaiming bare scalds in arid (less than 25 cm. annual precipitation) portions of New South Wales in Australia (Newman 1966). The treated areas were relatively flat and generally with less than 1-percent slope. The soils were deep clay to clay loam. Banks were constructed to pond water to depths of 15-25 cm. Good stands were obtained from seeding oldman saltbush (*Atriplex nummularia*), perennial saltbush (*A. vesicaria*), and several grasses.

Natural colonization of native plants has occurred on waterponded scalds near Nyngan, New South Wales (Cunningham 1970). The waterponding technique is based primarily upon handling of local water rather than that from outside areas. The water in each pond is from the actual rainfall on the ponded area, plus runoff from the small unponded catchment above each bank.

In New Mexico, Valentine (1947) studied five types of structures that retained runoff water. None of the structures were effective in improving the vegetation. Various soil factors were responsible for the failure of the structures.

Soil firming

Seedbed compaction can result in two opposite effects: (1) the water supply to seeds may be improved because of greater contact between seed and soil, and greater soil unsaturated conductivity, but (2) undesirable effects may result because of greater mechanical impedance to seedling emergence and root penetration as well as restricted aeration. One possible method to achieve optimal conditions is to compact the soil below the seeds and use loose soil above the seeds. A laboratory study, with no evaporation allowed, showed that compaction below the seeds improved emergence in some instances and reduced it in others. Compaction above the seeds reduced emergence in all trials (Tadmor and others 1968).

Trials in Israel indicated that *Atriplex halimus* could not emerge from a compacted surface (Koller and others 1958). Seeds were sown in moist, shallow furrows at a depth of 2-5 cm. In part of the furrows the covering soil was firmly packed while in others it was left loose. On drying, the packed soil formed a hard crust which most of the germinating seedlings were unable to penetrate. Full rows of seedlings appeared within 3-4 weeks after sowing in the loosely covered furrows.

Seeding of *Atriplex halimus* in heavy mud that had accumulated as a result of floods, behind dams and dikes, resulted in good establishment (Koller and others 1958). The seeds were broadcast 1-2 days after flooding.

The effects of cultipacking, prepacking, and postpacking on the establishment of crested wheatgrass seedlings were evaluated in northeastern Colorado by McGinnies (1962). Cultipacking prior to seeding increased the number of seedlings. Prepacking (wheel-track planting) improved seedling stands, but there was little difference in 32- or 136-kg. wheel pressures. Postpacking generally improved seedling stands but less than prepacking. If there was heavy pressure (136 kg.) on the packer wheel, it pushed the seed too deeply, and thus reduced seedling numbers.

Hyder and Bement (1969) designed a roller for firming and seeding light-textured soils. Interrupted furrows are formed to concentrate water on the seeded rows. Ridging of sandy loam soil by compacting with a heavy packer wheel prevented wind erosion from the modified seedbed (Marlatt and Hyder 1970). High intensity rain and hail did eliminate the ridges. A sandy loam soil should contain 9-12 percent moisture when packed to obtain a surface condition greatly resistant to wind erosion (Hyder and Bement 1970).

Plowing and seeding

A browse seeder has been developed that will plant an assortment of seeds on a variety of sites (Interagency Range Seeding Equipment Committee 1965). Various furrow openers, such as a moldboard and a scalper, may be used. Seed is planted immediately back of the furrow openers, and soil is firmed over the seed by a packer wheel. Furrow depth is controlled by depth regulators. The seeder has a fluted feed cylinder which has the desired grooves for seeds of different sizes and shapes. This method was used to successfully seed antelope bitterbrush (*Purshia tridentata*) in Idaho (Holmgren and Basile 1959). There, the purpose of the moldboard is to remove undesirable plants. The furrows are at least 0.8 m. wide and deep enough to prevent resprouting of perennial forbs. In Utah, drills equipped with scalpers (15-60 cm. wide) effectively eliminate weeds and provide a satisfactory method of seeding shrubs and perennial forbs in competitive annual types (Plummer, Christensen, and Monsen 1968).

Seeding native grasses at the time of rootplowing failed to provide satisfactory stands at several locations in the High Plains of Texas, where average annual precipitation ranges from 46 to 56 cm. (Jaynes and others 1968). Loss of plants after emergence was attributed to rapid depletion of soil moisture from the loose seedbed following rootplowing and to severe competition from weeds.

Fine sandy loam and gravelly sandy loam sites infested with brush were rootplowed on the Jornada Experimental Range where the average annual precipitation is 22 cm. This was followed by a till-and-pack seeder which pressed most of the brush into the soil. The maximum air temperature 10 cm. above the surface of the ground ranged from 29° to 34° C. during the latter half of July and the early part of September. During August it ranged from 38° to 40° C. The minimum relative humidity ranged from 27 to 57 percent during July and September, and 16 to 17 percent during August. Maximum soil temperatures at the 1.3-cm. depth averaged 51° C. with no ground cover and 38° C. under brush cover. A high temperature of 59° C. was recorded at the 1.3-cm. depth with no surface cover and 41° C. under brush cover. During an 82-day period, 12 cm. rainfall was recorded July 2-August 3 on the fine sandy loam site, followed by 2.3 cm. on September 7. Moisture potential at the 1.3-cm. depth was between 0 and -15 bars for 5 days on the area with no cover and 42 days on the area with brush cover (fig. 4). On the gravelly sandy loam site there were 8.6 cm. rainfall July 2-August 3 and 2.8 cm. on September 7. Moisture potential at the 1.3-cm. depth was between 0 and -15 bars for 23 days on the area without cover and 40 days on the area with brush cover (fig. 5). Poor seedling establishment was obtained with this seeding, primarily because of the severe environmental conditions in August (Herbel 1972).

The effects of dead shrubs on soil temperatures were studied on a fine sandy loam site on the Jornada Experimental Range. A single shrub plant was used for the light plant cover and a layer of three shrubs for the heavy cover. The average maximum air temperature 10 cm. above the ground surface for a summer period was 33° C. The average daily maximum soil temperature at the 1.3-cm. depth was 57° C. under no cover, 49° C. under light cover, and 36° C. under heavy brush cover (fig. 6) (Herbel 1972).

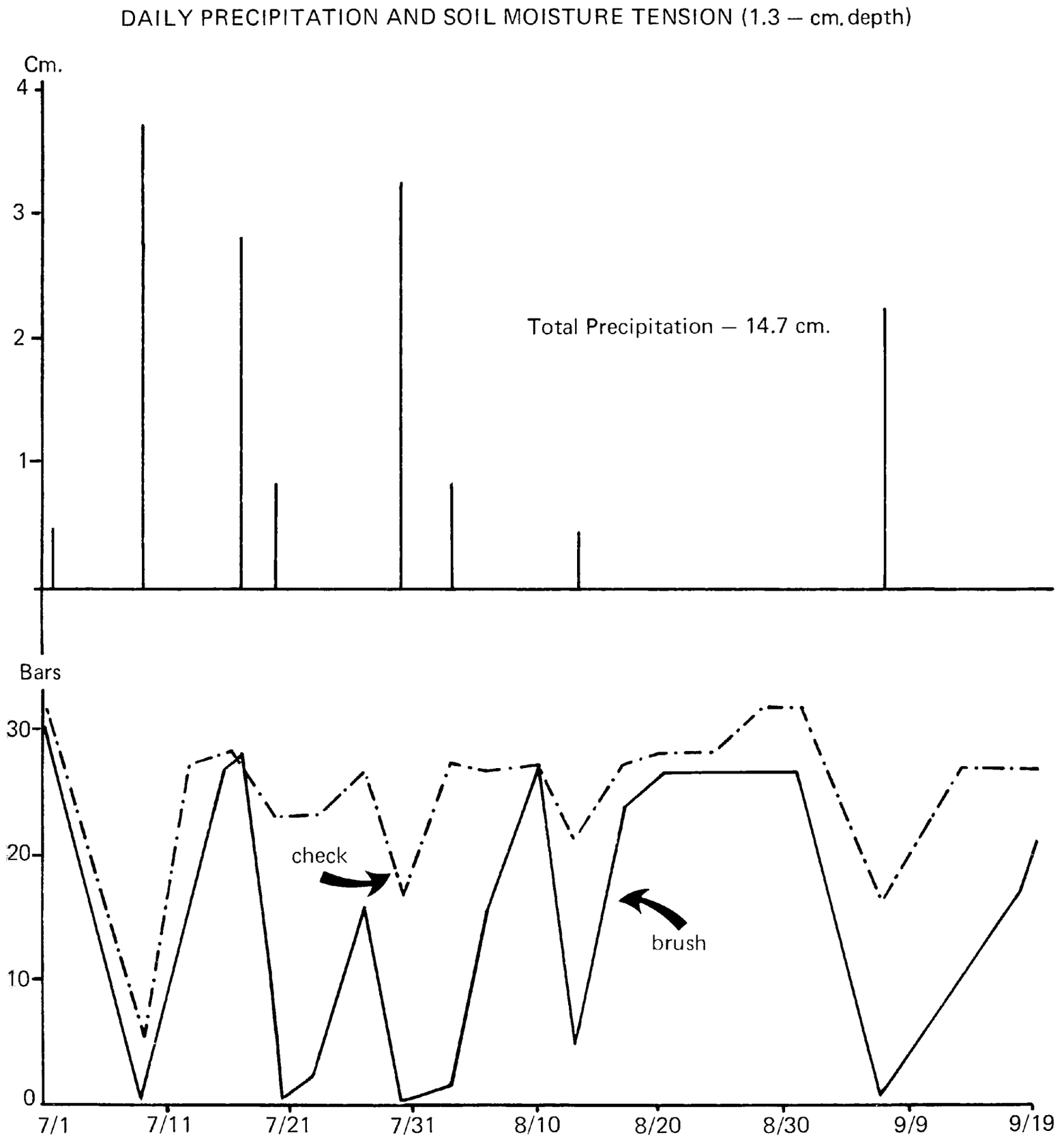

Figure 4.--Daily precipitation (cm.) and soil moisture potential (bars) at the 1.3-cm. depth without surface cover and under brush cover on a fine sandy loam site on the Jornada Experimental Range (Herbel 1972). The area was root-plowed and seeded with a till-and-pack seeder on June 25, 1962. Soil moisture was recorded twice weekly during the period July 2-September 20.

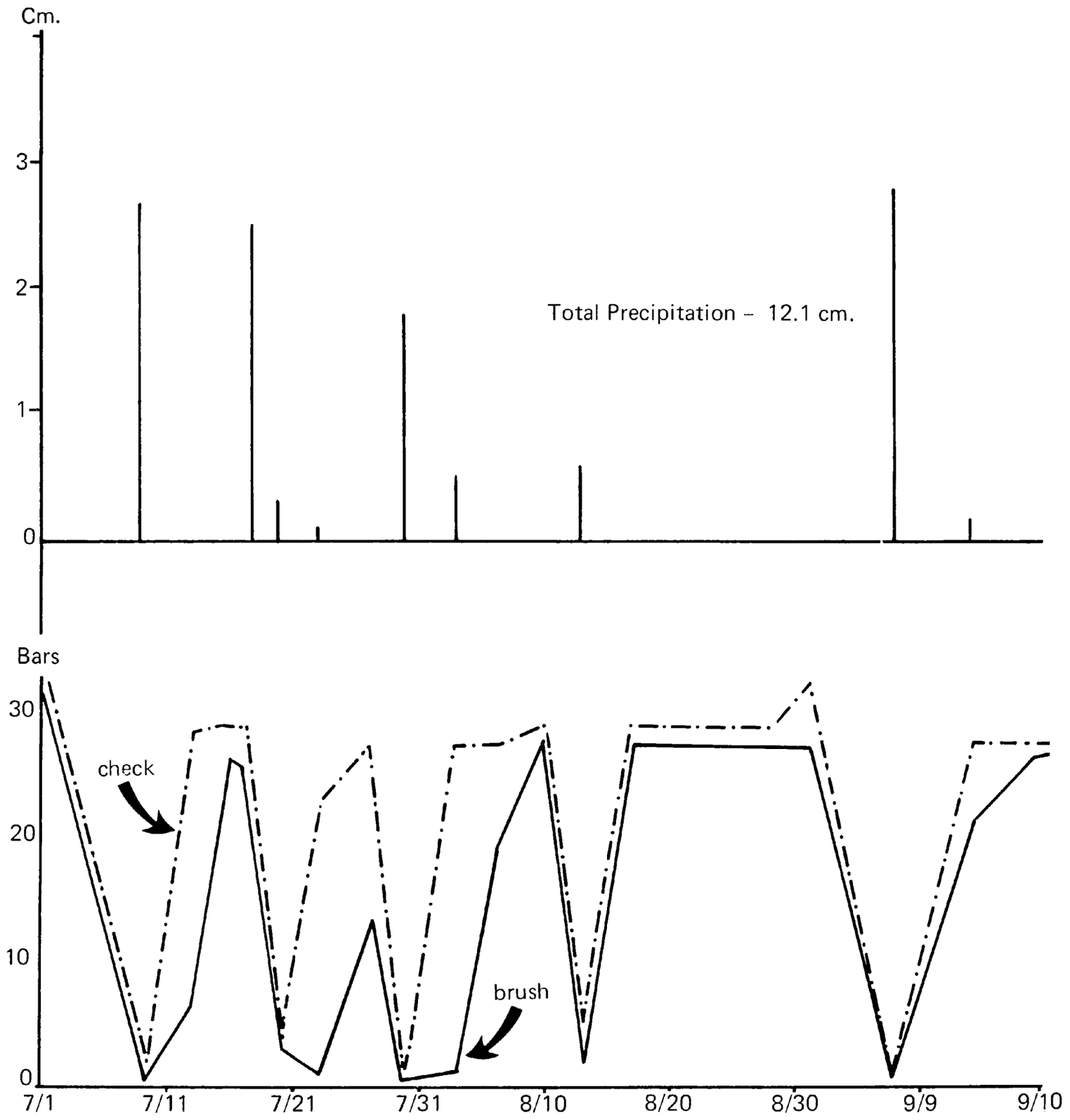

Figure 5.--Daily precipitation (cm.) and soil moisture potential (bars) at the 1.3-cm. depth without surface cover and under brush cover on a gravelly sandy loam site on the Jornada Experimental Range (Herbel 1972). The area was root-plowed and seeded with a till-and-pack seeder on June 25, 1962. Soil moisture was recorded twice weekly during the period July 2-September 20.

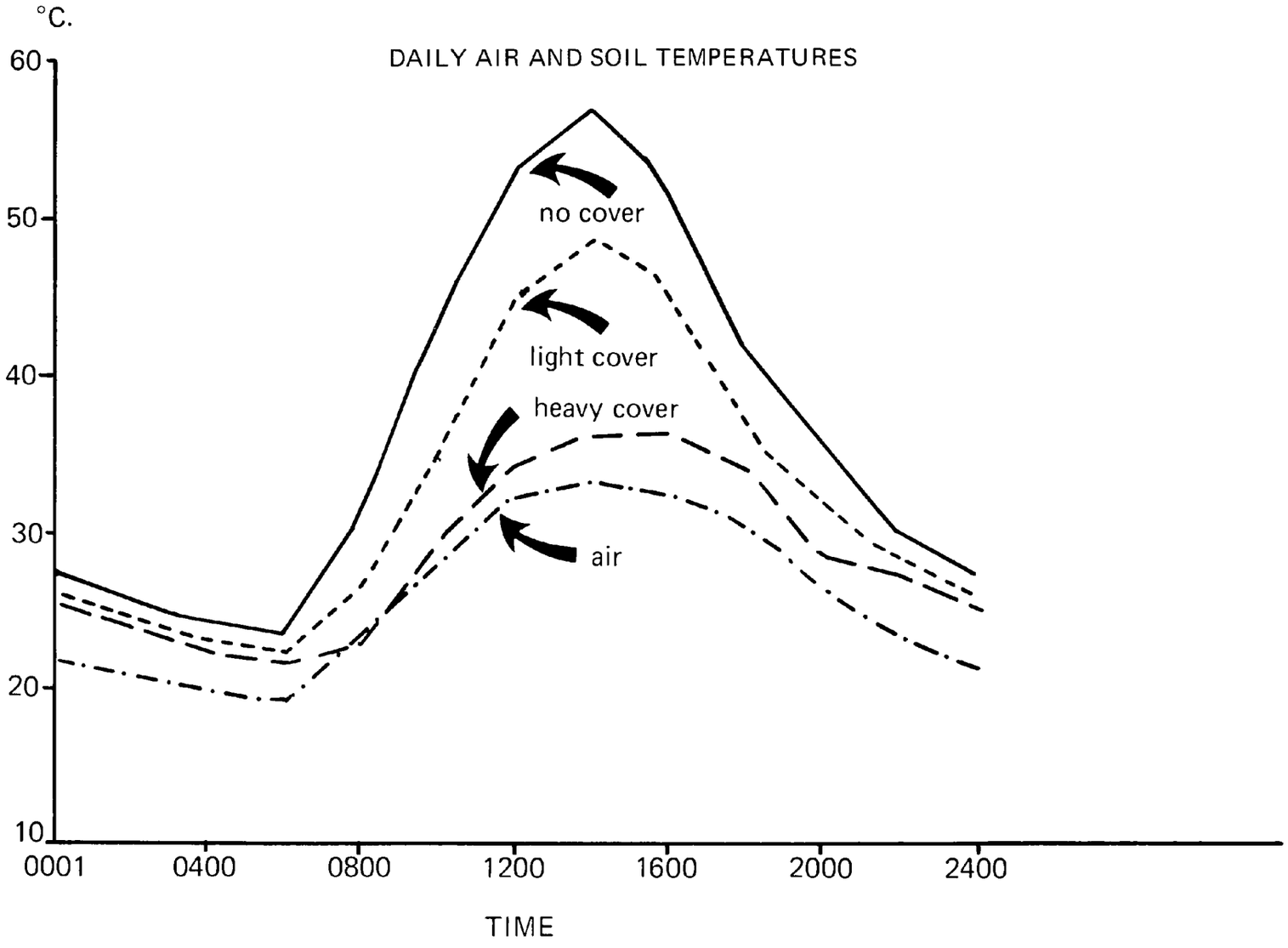

*Figure 6.--Average daily soil temperatures (°C.) at the 1.3-cm. depth with light and heavy brush cover, without surface cover, and air temperature 10 cm. above the surface of the soil for the period July 28-August 15, 1964, on the Jornada Experimental Range (Herbel 1972). Light brush cover = one dead tarbush (*Flourensia cernua*) plant; heavy brush cover = three dead tarbush plants.*

A light chamber study elucidated the effects of soil temperatures, observed under field conditions, on emergence and initial growth of 12 grass species and fourwing saltbush (*Atriplex canescens*) in a soil medium (Sosebee and Herbel 1969). The two maximum daily temperatures were 39° and 53° C., and the soil moisture was maintained at field capacity. The emergence of fourwing saltbush was 0.5 percent in the high temperature regime and 170 percent of viable seed, as determined by a standard germination test, in the low temperature regime. The latter indicated a more favorable environment than conditions considered "optimum" in a standard laboratory germination test. There was no survival of emerging seedlings of fourwing saltbush after 21 days in the high temperature regime and 98 percent survival in the low temperature regime. The plant height and root length after 21 days in the low temperature regime was 5 and 11 cm., respectively. In a similar study, but with various moisture levels, it took 7 cm. of water for survival of two grass species in the low temperature regime and 23 cm. for survival in the high regime in a 21-day trial (Herbel and Sosebee 1969).

We found that brush cover could be utilized to reduce soil temperatures substantially, and increase the period of available soil moisture. Subsequently, in cooperation with Dr. George Abernathy, Agricultural Engineering Department at New Mexico

Figure 7.--Root plow, brush conveyor, pitter, and seeder for converting areas infested with noxious brush to areas producing useful vegetation. The brush conveyor is operated by a hydraulic motor and the height of the pickup unit is hydraulically controlled. The basin pits are made with a hydraulically-controlled bulldozer blade. The press-wheel seeder firms the soil prior to seeding. The brush conveyor and pitter were designed and developed by Dr. George Abernathy, Agricultural Engineering Department, New Mexico State University.

State University, we developed and tested equipment for seeding rangeland infested with brush (fig. 7). The brush and other competing vegetation are controlled with a root plow with a blade 2.4 m. wide. The rootplowed seedbed is very loose and fluffy. Then we designed a seeder, patterned after the Oregon Press Seeder (Hyder and others 1961), which firms the soil. The seed is placed in a V-shaped groove pressed into the soil. Drag chains cover the seed with loose soil to a depth of about 1.3 cm. A brush conveyor was then developed that picks up the brush behind the root plow and deposits it behind the seeder. The seeder is only 1 m. wide, so the brush from a 2.4-m. area is concentrated on a strip 1 m. wide. In addition, there is a hydraulically-operated bulldozer blade in front of the seeder that forms basin pits. Thus, we were able to concentrate water and provide shade for part of the seeded area. This method was used to seed 12 plots across southern New Mexico in 1967-68. A variety of grass species and fourwing saltbush was seeded on each plot. Good to excellent establishment was obtained on nine of the 12 plots. Even on the other three plots with droughty conditions, good stands were obtained under some of the brush cover, which coincided with slight depressions where water was concentrated (Herbel 1971). Virtually all the establishment of fourwing saltbush occurred under brush cover, even on the sites that had above-average precipitation.

Conclusions

The major objectives of preparing seedbeds for range seeding are: (1) to prepare a favorable microenvironment for seedling establishment, (2) remove or substantially reduce competing vegetation, and (3) if possible, leave litter on the surface of the soil to reduce erosion hazards and to improve the microclimate. Broadcasting is the

poorest method of seeding, particularly on unprepared seedbeds. Some form of plowing or otherwise mixing the surface soil with the soil from deeper depths may create a more favorable environment. The deeper soils often have a higher level of nutrients, a more favorable microbiota and, in the case of sandy soils, a higher capacity for holding moisture.

Only limited seeding success was obtained following pitting with a pitting disk and ripping. Ripping lines often seal over in a relatively short time. Narrow pits can fill with soil rather rapidly on some sites. Part of the problem with pits made with a pitter disk is that the cut made by the disk is smooth and slightly compacted and, therefore, a poor environment to obtain seedling establishment. In pitter disk seeding, the seeds are generally broadcast in the pitted area and covered somewhat by use of drag chains. Whitney and others (1967) used opener blades and a packer wheel to improve pitter disk seeding. In a grass sod, the pitter disk often does not reduce competition sufficiently to permit establishment of seeded species. In areas where there is a natural supply of seed of desirable species, pitting or furrowing provides a good seedbed for an increase of plants growing in the vicinity.

The broad, shallow pits made with the basin-forming machine developed by Frost and Hamilton (1965) made a good seedbed. A similar procedure is to make pits with a bulldozer blade (Moore 1960). Pitting is generally most successful on medium- to heavy-textured soils on flat or gently sloping sites.

Contour furrows form good seedbeds on medium- to heavy-textured soils. It is desirable to use interrupted furrows (1) to prevent a large water loss if a furrow wall breaks and (2) to preclude the necessity of furrowing exactly on the contour. On slopes, it would be desirable to leave spoil from the furrow on the downslope side. Considerable research is needed (1) to determine optimum furrow shape for different soil types and slopes, (2) to study the possibility of seeding on the slope of the furrow, and (3) to determine the proper orientation for furrows at various locations. In Wyoming, furrow seeding increased the yield of the native Nuttall saltbush as well as yielding a substantial amount of the seeded grass (Nichols 1964).

Waterponding of relatively large basins was effective in reclaiming bare scald areas both from seeded species (Newman 1966) and from natural colonization of native plants (Cunningham 1970). This practice, and basin pits, may have considerable application for substantially increasing herbage yields on relatively flat (0-1 percent slopes) areas.

Soil firming beneath the seed was more successful than firming the soil surface after seeding in most trials. Firming the soil after seeding has these disadvantages: (1) It may push the seed deeper then desired, (2) it may restrict aeration in the seed zone, and (3) it enhances crusting on some soils. A successful method of seeding on some sandy soils is to firm the soil into interrupted furrows (Hyder and Bement 1969).

A method of seeding arid areas infested with brush has been discussed by Herbel (1971). The brush and competing vegetation are controlled by a rootplow. Basin pits are formed and about 40 percent of the area is seeded with a press-wheel seeder. An attempt is made to concentrate the brush and water on the seeded area. Brush control, pitting, seeding, and brush placement are accomplished with one pass over the land.

Concentrating water, as with various land-forming procedures, does not always insure seedling establishment. The surface soil still dries rapidly, particularly in hot arid and semiarid areas. This rapid drying may lead to the formation of a heavy crust on medium- to heavy-textured soils. In those instances, if the surface could be protected to reduce evaporation, seedling emergence and establishment would be greatly enhanced.

Using mulches to establish woody chenopods

H. W. Springfield

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Establishing shrubs by direct seeding is full of uncertainties, especially in the arid and semiarid zones. During the rainy season, when soil moisture is more likely to be adequate, temperatures often are either too high or too low. And, when temperatures are near optimum, soil moisture often is deficient. Optimum soil moisture and temperature for seed germination and seedling growth seldom occur simultaneously for more than a few days. To improve the chances of success from seeding, the microenvironment must be manipulated to provide more nearly optimum conditions for a longer period of time.

Recently Herbel (1971) emphasized that environmental modification, particularly of the moisture and temperature, is imperative to insure greater success in grass establishment. Similarly, Cohen and Tadmor (1969) suggest some agrotechnical means be employed to warm up the seedbed where the combination of low temperatures and low rainfall make the success of range seeding operations uncertain.

Mulching is one of several means of modifying the microenvironment to meet the needs of the seed and the seedling. The Hebrews used gravel mulches in the Sinai Desert thousands of years ago (Corey and Kemper 1968). Likewise, using pebble mulches in China dates back to antiquity (Cannon 1966). Spreading stones or straw on the ground to conserve moisture, and also reduce wind erosion, is an age-old practice of wheat and barley cultivators in the arid zones (Walton 1969).

Most of the available information about mulching relates to increased crop yields. The benefits of mulching on crop yields have been attributed to the conservation of moisture by reducing evaporation and runoff, protection from erosion, increased infiltration, suppression of weed growth, improvement in soil fertility, or the increase or decrease of soil-temperature fluctuations (Jacks and others 1955).

The effects of mulching on plant establishment are not as well documented, but there is evidence of worldwide interest. Nearly all of the recent information deals with using various plastic mulches to improve stands of vegetables. Only a fraction of this information can be considered pertinent to the problem of establishing shrubs on wildlands. Likewise much of what has been learned about using mulches to establish field crops is beyond our interest.

Our objectives here are to (1) describe the functions of various types of mulches reported in the literature, and (2) discuss the results of mulch tests for establishing shrubs in the southwestern United States.

Types of mulches

Mulches may be conveniently classified as natural or synthetic (manufactured). Two of the most commonly used natural mulches are straw and hay; both can be spread and anchored readily with mechanical equipment. Other natural mulches include leaves, peat, sawdust, woodchips, manure, brush, gravel, and stones. A form of mulching commonly practiced in the Great Plains, stubble mulching effectively controls erosion and conserves moisture, but problems are encountered in machine operation, weed control, insufficient residues, and toxic effects (Woodruff and others 1966).

Synthetic mulches include organic and inorganic liquids that can be sprayed on the soil surface to form a thin film, such as resin or asphalt emulsions, latex, and cutback asphalt (Chepil and others 1963). Also included are canvas, burlap, and a variety of plastic materials, such as polyethylene and polyvinyl chloride (Spice 1963).

Straw and other natural vegetative mulches usually reduce evaporation of soil moisture, prevent crusting of the soil surface, reduce soil temperature fluctuations, improve infiltration, and control runoff. In India, for example, mulching with straw gave better stands of cereal grains due to improved infiltration and moisture conservation (Choudhary and Chatterjee 1967). In Rhodesia, establishment of dryland pasture was improved by mulching with old veld hay which prevented soil crusting (Smith 1966). Of several mulches compared in Texas, straw mulch proved most effective in retarding evaporation, increasing infiltration, and minimizing raindrop impact (Adams 1966).

Extensive tests in southern New Mexico demonstrated the advantages of a brush mulch for establishing perennial forage species on root plowed ranges (Herbel 1971). The brush mulch reduced soil moisture losses and lowered daytime temperatures.

The variety of plastic mulches available afford unique opportunities for modifying soil conditions (Spice 1963). Unfortunately, most plastic films are difficult to apply and are too expensive for use on wildlands, except for very critical areas.

Petroleum mulches, on the other hand, are easier to apply and less expensive. Various petroleum mulches were used in horticulture 30 years ago and have been used many years for establishing grass along roadsides, but new formulations have led to a revival of their use for both seedling establishment and soil stabilization (Sale 1966). Most formulations are emulsions of asphalt in water that can be sprayed on the soil at ambient temperatures to form a thin, continuous film that clings to the soil but does not penetrate deeply (Black and Popkin 1967). Besides being easily applied as a spray, petroleum mulch forms a film that is tight, yet pliable and readily penetrated by seedlings (Adams 1967). When functioning properly, the mulch film promotes uniform, rapid seed germination and vigorous seedling growth. A number of investigators have reported a thin layer of asphalt mulch improves seedling emergence by preventing surface crusting (Adams 1967; Tadmor and others 1968). In several experiments, petroleum mulching has effectively raised soil temperatures to allow earlier than normal seeding (Takatori and others 1964; Cannon 1966; Miller 1968).

Petroleum mulches have been tested in many countries, besides being used commercially in the Western United States. In Russia, petroleum mulch conserved moisture, prevented soil crusting, and resulted in faster emergence and better growth of cotton seedlings (Abdurakhimov and Solovyev 1968). In India, grass establishment was improved where a water emulsion of petroleum resin was sprayed over seeded rows (Roy and Chatterjee 1965). Results of more than 100 field trials in France, Italy, England, and Trinidad showed petroleum mulches increased soil temperatures, reduced soil moisture losses and protected soil surfaces from rain damage (Nyns 1967; Jordan and Sampson 1966).

In one of the few studies on wildlands, asphalt-emulsion mulches hastened the emergence and development of blue grama (Bement and others 1961). Results from these

range studies in Colorado showed soil moisture was maintained for a longer period and soil temperatures were higher under asphalt, compared with unmulched areas. A similar study on wildlands in Israel showed petroleum mulching increased the daytime temperatures considerably; this increase resulted in a 2- to 5-day hastening of germination and emergence of grass species (Tadmor and others 1968).

With few exceptions, petroleum mulch--as well as the other synthetic mulches--has been used to raise soil temperatures. Asphalt, being dark in color, absorbs more solar radiation than most soils; as a rule, the thicker the asphalt, the higher the temperature of the soil underneath. If the asphalt is painted white, however, the soil temperature is lowered--even lower than the bare soil (Collis-George and others 1963). Similarly, either white- or aluminum-pigmented plastic film brings about lower soil temperatures due to reflection of incident sunlight (Waggoner and others 1960).

White- to cream-colored petroleum resin emulsions proved effective for establishing vegetables when air temperatures were 35° to 37° C. (Gerard and Chambers 1967). White polyethylene perforated over the seeded row gave an excellent stand of grass seedlings, compared with only a sparse stand in check furrows in southern New Mexico (Herbel 1972). Soil temperatures in the seed zone were 10 to 18 degrees cooler in hot, sunny weather, and soil moisture remained adequate for more days under the white film.

Mulch tests with shrubs in the Southwest

Mulching has been studied at the Rocky Mountain Station as a method for establishing woody chenopods in the southwestern United States. Included in these studies were fourwing saltbush *(Atriplex canescens* (Pursh) Nutt.) and winterfat (*Eurotia lanata* (Pursh) Moq.).

In several preliminary tests, native grass over seeded rows usually resulted in better stands of fourwing saltbush and winterfat under a variety of environmental conditions. In a few instances where mulching proved of no benefit, the rate of application was judged to be too heavy. In other instances, the effects of mulches were judged to be insufficient to compensate for a prolonged period of dry, windy weather. Because neither soil temperature nor soil moisture was measured in these preliminary tests, the results were subject to some speculation. The beneficial results from mulching in most of these tests, however, stimulated further investigations.

A series of experiments conducted from 1967 through 1970 near Santa Fe, New Mexico, were aimed at modifying the microenvironment to meet the needs of the shrub seed and seedling. The basic concept was to plant the seed in moist soil, then apply a mulch that not only delayed moisture losses from the soil but also provided near-optimum temperatures in the seed zone. Information from a number of experiments defined the optimum temperatures and moisture for germination and proper depth of seeding for both species (Springfield 1966, 1968, 1970a, 1970b). Seeds of fourwing saltbush and winterfat germinate best at temperatures from 13° to 24° C. and at osmotic stresses of three atmospheres or less. Fourwing saltbush seeds should be planted 13 to 25 mm. deep; winterfat seeds, 2 to 3 mm.

Procedures for all mulching experiments were similar. Seeds were planted in shallow furrows at the rate of 50 viable seeds per meter of row. Soil moisture was near field capacity at the time of seeding. Mulches were applied immediately after seeding. Included as mulches were: straw, white petroleum resin (WPR),[1] and Soil

[1]Experimental product supplied by Dr. R. L. Ferm, Chevron Research, Richmond, California. White petroleum resin, 68R-5268, a dispersion of a white pigment in a petroleum derived resin aqueous emulsion. Company and trade names are used for the benefit of the reader, and do not imply endorsement or preferential treatment by the U.S. Department of Agriculture.

Gard.[2] Straw was applied by hand, whereas the liquid mulches were applied with a pressure sprayer, calibrated volumetrically. Mulches were in bands about 25 cm. wide. Soil moisture was determined by gravimetric sampling and by calibrated gypsum blocks. Soil temperatures were measured by thermistors placed in the test rows at the same level as the seeds and covered with the same amount of soil and mulch material.

1969 Studies

In 1969, three mulch studies were conducted: two with fourwing saltbush and one with winterfat. Mulches were applied, immediately after seeding, at these rates:

Rate per 100 meters of row	*Light*	*Medium*	*Heavy*
Straw (kg. air dry)	2.3	4.7	7.0
WPR (liters, not diluted)	13.2	26.3	39.5
Soil Gard (liters, 1:9 dilution)	12.9	25.8	38.7

The first study with fourwing saltbush was conducted during hot, dry, windy weather from June 24 to July 20, 1969. Rainfall from showers totaled less than 3 mm. The mulches only slightly retarded moisture losses from the top 1.3 cm. of soil, which dried rapidly during the first week after seeding (fig. 1). The advantages of mulching became evident the 5th and 6th days. Slightly but significantly more moisture was available to the germinating seed and developing seedlings in mulched than in unmulched rows. By the 7th day, soil moisture tensions exceeded 15 atmospheres in all rows. Nevertheless, a few saltbush seedlings emerged. Rate of mulch application had no effect on emergence. By the 20th day, seedlings per meter of row numbered 2.0 for WPR, 1.6 for straw, and 0 for Soil Gard and no mulch. High soil temperatures no doubt explain why seedlings failed to emerge in rows mulched with Soil Gard. Temperatures in the seed zone at 1400 hr. on the 6th day--a most critical time for the seeds and seedlings--were as follows (averages of three application rates):

	°C.
Air (shade)	34
Straw	33
WPR	27
Soil Gard	47
No mulch	45

Midafternoon soil temperatures during the first week measured 14 to 19 degrees cooler under WPR and 6 to 16 degrees cooler under straw than in bare soil. Cooler temperatures in combination with slightly more moisture available when needed by the germinating seeds account for the seedlings that emerged in rows mulched with WPR or straw.

The second study with fourwing saltbush, installed July 25, 1969, was conducted during cool, moist weather. As a consequence, neither soil temperatures nor soil moisture tensions reached high levels. Nevertheless, certain mulch treatments resulted in significantly better seedling establishment, presumably by providing a better micro-environment for the seeds and seedlings. Soil moisture tension, for example, generally

[2]A pigmented latex compound manufactured by Alco Chemical Corp., Philadelphia, Pa.

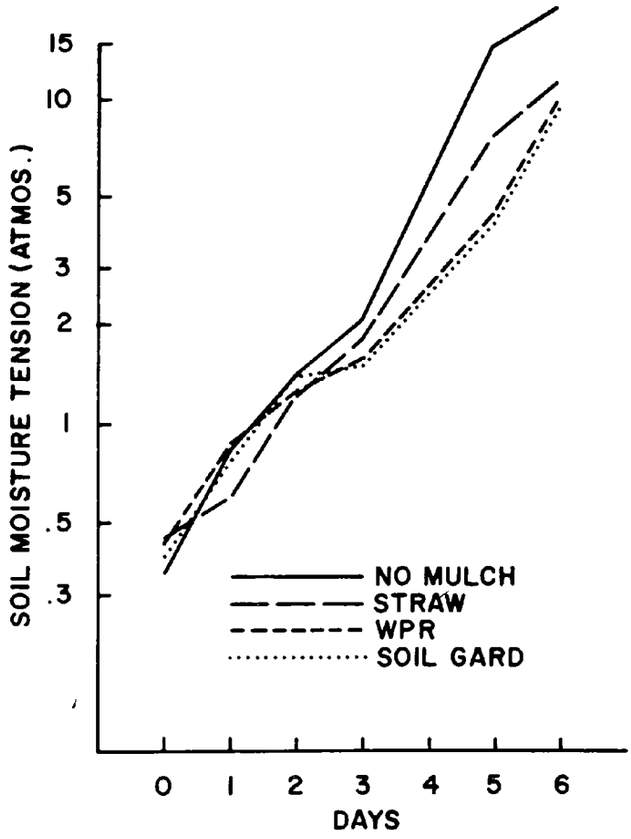


Figure 1.--Soil moisture tensions during the first 6 days of the mulch study begun 6/24/69 (averages for three application rates).

was less under straw and WPR than in bare soil throughout the experiment. But even when the tension was highest--the 5th day--the difference was not great: 1.4 atm. under straw and WPR as against 3.2 atm. in bare soil. Soil temperatures remained comparatively low nearly every day. For example, during the first week, temperatures at 1600 hr. averaged as follows:

	°C.
Air (shade)	31
Straw	31
WPR	28
Soil Gard	41
No mulch	37

Seedling establishment was good regardless of mulch treatment. The greatest number of seedlings became established in rows mulched lightly with straw:

Mulch		*Seedlings per meter of row*
Straw	Light	18.5 a[3]
	Medium	14.5 ab
	Heavy	11.6 bc
WPR	Light	15.2 ab
	Medium	11.6 bc
	Heavy	9.2 c
Soil Gard	Light	9.6 c
	Medium	4.6 d
	Heavy	3.6 d
No mulch		10.2 c

[3]Means followed by the same letter are not significantly different at the 5 percent level.

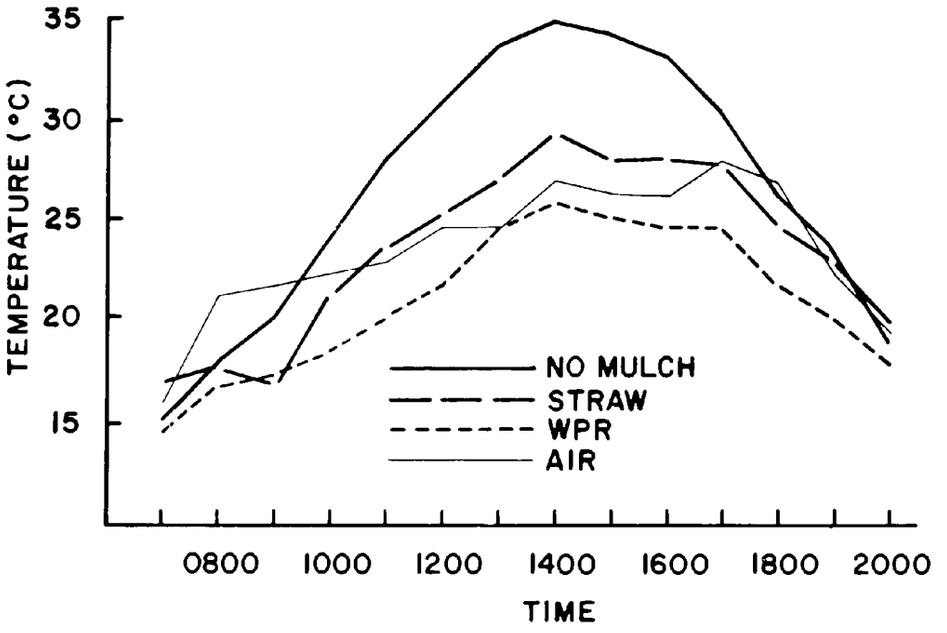


Figure 2.--Soil and air temperatures during the first week of the 1969 winterfat mulching study.

The light rate of straw resulted in 3.3 seedlings more per meter than the light rate with WPR, a difference statistically significant at the 10 percent level. Seedling stands in rows mulched with straw at the medium rate and with WPR at the light rate were better than stands in unmulched rows.

The third study in 1969--with winterfat--was begun August 25. Straw and WPR at the medium rate were compared with no mulch in six randomized blocks. Emergence and establishment were better where mulch was applied:

	Straw	*WPR*	*No mulch*
	Seedlings/meter of row		
1 week	3.6	5.6	2.6
1 month	5.9	8.9	5.3
1 year	5.3	6.3	2.6

Seedlings began emerging the 5th day. Stands in rows mulched with WPR were consistently better than those in straw-mulched rows. The greater number of seedlings where WPR was applied may be explained by lower temperatures and generally less soil moisture tension. Temperatures under WPR were cooler than under straw (fig. 2). Likewise, soil moisture tension in the seed zone usually remained less in rows mulched with WPR.

1970 Study

In 1970, winterfat seeds were planted in moist soil and mulches applied June 24. Rates of mulch application were about the same as in 1969. Seedlings began emerging the second day. Seedling stands were significantly better in rows mulched with straw or WPR than in unmulched rows. Seedling stands developed as follows (average for three rates of application):

Days	*Straw*	*WPR*	*Soil Gard*	*No mulch*
	Seedlings/meter of row			
2	0.7	1.6	0	0
5	1.3	2.6	1.0	0.7
8	2.3	2.6	1.0	2.0
12	3.6	3.0	1.0	1.6
26	4.3	3.3	1.0	1.3

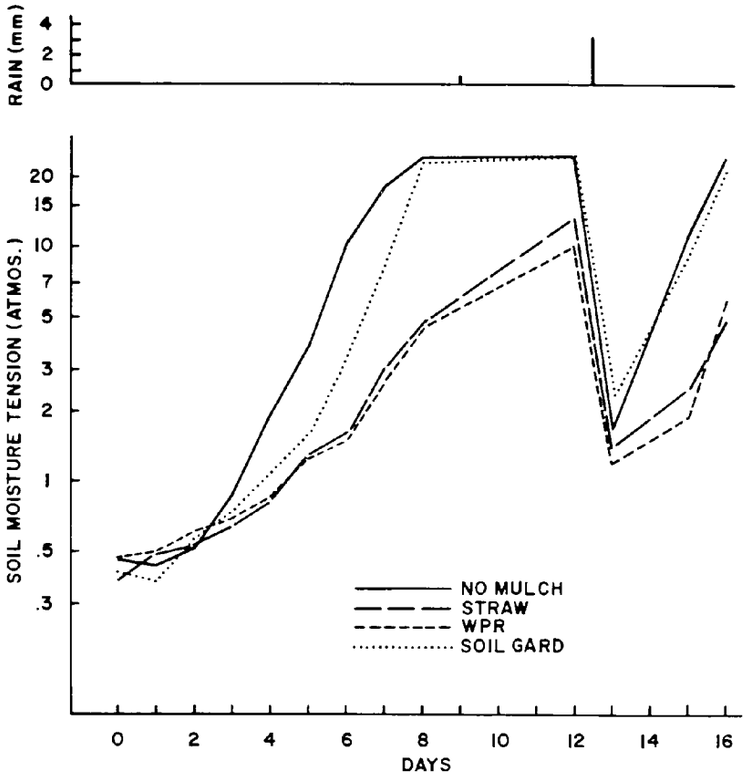


Figure 3.--Trends in soil moisture tension in mulched and unmulched rows during the first 16 days after application 6/24/70.

Although some winterfat seedlings emerged in the unmulched rows, the stands peaked by the 8th day, then declined. On the other hand, stands in rows mulched with straw or WPR continued to improve.

The essentially rainless period of 12 days after seeds were planted provided a good test of the effectiveness of the various mulches. On the day the mulches were applied, soil moisture tension ranged from 0.37 to 0.47 atm. After 5 days of dry weather, moisture tensions were 1.3 to 1.6 in mulched soil compared with 3.8 atm. in unmulched soil (fig. 3). On the 7th day, soil moisture tension measured 2.7 atm. in rows mulched with WPR compared with 18.0 atm. in unmulched rows. A 3.3 mm. rain July 6 (12th day) lowered moisture tensions in all soils, but by the 16th day, tensions exceeded 20 atm. in unmulched rows, 4.8 atm. under straw, and 5.9 atm. under WPR.

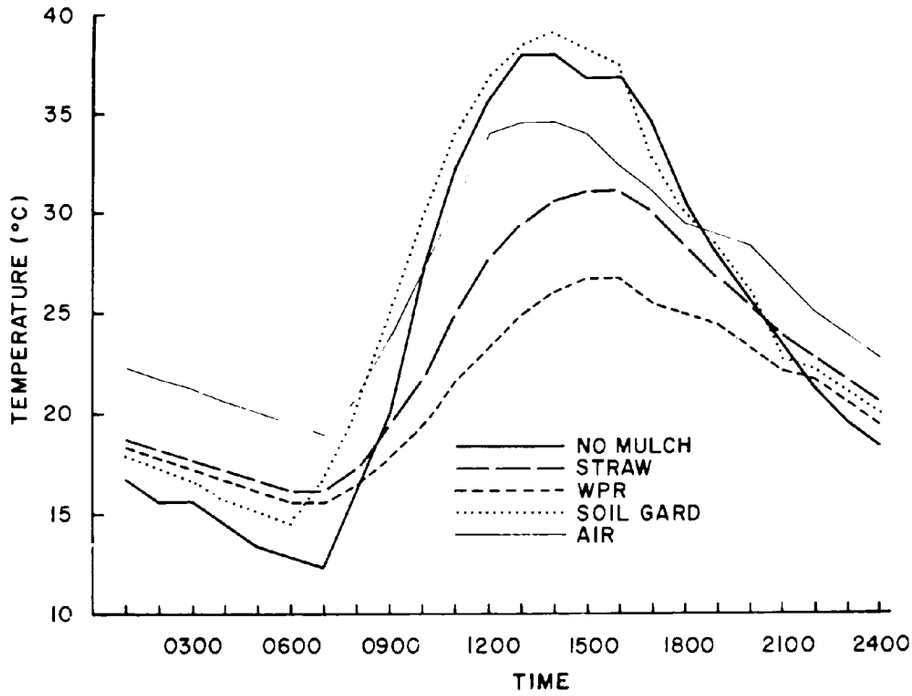


Figure 4.--Soil and air temperatures during the first 8 days after application 6/24/70.

Differences in temperatures under the three kinds of mulch also help explain the differences in seedling emergence (fig. 4). During the first 8 days--which no doubt were critical days for the germinating seeds and emerging seedlings--soil temperatures under Soil Gard exceeded 38° C. every afternoon. The unmulched soil also reached 38° C. several times. In sharp contrast, soil temperatures remained mostly less than 26° C. under WPR--the highest recorded under WPR was 27.2° C. Temperatures beneath straw mulch likewise were relatively cool. Of interest is the 2-hr. lag under the WPR and straw; highest air temperatures were recorded at 1300 and 1400 hr., which corresponded to the time of day when unmulched soil was hottest, but under WPR and straw, temperatures were highest at 1500 and 1600 hr. Temperatures usually reached their lowest at 0600 or 0700 hr. At 0700 hr., the unmulched soil averaged only 12° C. compared with temperatures of 19° C. for the air and 16° C. for soil mulched with straw.

Discussion

The results of these studies at Santa Fe support the basic concept of modifying the microenvironment to meet the needs of the seed and seedling. Seeds of fourwing saltbush and winterfat should be planted shallow and require relatively moist soil and cool temperatures for germination. The chances are slim that cool, moist conditions will prevail naturally in the top layers of soil for several consecutive days during the summer in the Southwest. The chances of successful seeding are much improved if the seeds are planted in moist soil and then a mulch, such as straw, is applied to delay moisture losses and reduce soil temperatures. Sometimes only a slight benefit for a day or two may be enough to tip the balance in favor of seed germination or subsequent seedling survival.

Although mulching consistently resulted in seedling emergence in the Santa Fe studies, followup rains were essential for successful plant establishment. Thus, rain is needed to provide moist soil for the initial seeding-mulching operation, and rain is needed later to keep the seedlings alive and growing. All of the experimental seedings were made during the summer season because rains are far more dependable in summer than during other seasons in the Southwest. Due to higher solar radiation in summer, the mulch should be reflective (straw and WPR in the Santa Fe studies). If the mulch absorbs radiant energy and transmits it downward, temperatures in the seed zone may be so high that germination is inhibited. This characteristic could be an advantage for seeding during cool seasons. For example, the seeds might be placed in moist soil in the early spring when temperatures are low, then covered with a dark material such as Soil Gard or black petroleum mulch.

Mulches with reflective properties proved most effective in the Santa Fe studies, chiefly because of the requirement of the woody chenopod seeds for relatively cool temperatures. A thin coating of almost any reflective material can be expected to lower soil temperatures, and at the same time reduce the moisture tensions to which seeds might be exposed.

The effect of a mulch on seedling establishment will depend on soil texture, intensity of seedbed preparation, weather before, during, and after mulch application, thickness and width of the mulch material over the seeded row, and certain properties of the mulch itself. For example, asphalt films usually are stable and remain intact several months on sandy soils, whereas on silty clay or clay soils they disintegrate within 2 to 12 weeks because of the swelling and contracting of the soil (Chepil and others 1963). A smooth surface, containing a minimum of coarse fractions, requires less material and results in a better film (Cannon 1966). High-intensity rainstorms tend to break up an asphalt film and reduce its moisture-holding capacity (Bement and others 1961). Petroleum mulch will collect dust, which changes its absorptivity or reflectivity. The white petroleum resin, for example, became largely ineffective for temperature control within 4 to 6 weeks in the Santa Fe studies due to accumulation of soil over the surface and partial disintegration of the film.

The various synthetic mulches, such as the white petroleum resin used in the Santa Fe studies, have several desirable characteristics. For one, their application can be mechanized and combined with seeding operations. For another, the material does not injure seedlings and, at the rate of 1.4 $m.^3$/ha. sprayed in bands 30 cm. wide over rows 1 m. apart, there have not been any chemical or physical problems in the soil (Miller 1968). Also the width of the sprayed band can be easily varied and regulated. A 15-cm. band appears to be the minimum effective width from the standpoint of soil moisture temperature, and plant response (Lippert and others 1964). Band widths of less than 15 cm. fail to modify soil temperatures because of rapid conduction of heat along the edges as well as limited absorptive or reflective surface.

The ideal surface film would be stable against erosion, sufficiently porous to allow water to enter, yet insoluble in water and resistant enough to the forces of weather that it lasts as long as is necessary for permanent vegetation to become established. Next to well-anchored vegetative covers, resin-in-water emulsions come closest to meeting these requirements, according to Chepil and others (1963). Resin-in-water emulsions, of which the WPR used at Santa Fe is an example, are highly stable and can be diluted with large quantities of water without breaking the emulsion. The film is especially stable on sandy soil, but disintegrates within a few weeks on silty clay or clay soil. Emergence of seedlings generally is better through resin-in-water film than through asphalt or latex films.

Latex film, represented by Soil Gard in the Santa Fe experiment, generally resulted in poor establishment and growth of shrub seedlings. The dark green elastic coating not only created high temperatures in the seed zone, but also appeared to physically hinder seedling emergence, especially at the higher rates of application.

Conventional mulches that function largely through a "blanket" of still air are distinctly different from petroleum mulches that are in intimate contact with the soil surface (Collis-George and others 1963). Differences in the effects observed presumably relate to the presence or absence of the "blanket" of still air.

In addition to conserving moisture and reducing soil temperature fluctuations, straw or hay mulches protect the soil surface from raindrop impact and hold excess surface water in contact with the soil so as to increase infiltration and reduce runoff (Adams 1966). During the day a straw or hay mulch will absorb as much insolation as bare soil, but little energy is conducted downward; the surface of the mulch becomes hot but the soil remains cool. During the night the mulch cools, while permitting the soil to remain warm (Waggoner and others 1960).

Observations at Santa Fe during June 1969 indicated that hot, dry, windy weather reduced the effectiveness of all mulches studied, regardless of rate of application. Experiments in a wind tunnel (Hanks and Woodruff 1958) showed that a surface layer of dry soil was more effective than gravel or straw mulch in preventing soil moisture losses; evaporation was proportional to windspeed.

Weed control may be a problem in mulching. Chemical weed control is being evaluated by incorporating herbicides into synthetic mulches, particularly plastic films (Nakayama and others 1968); this offers possibilities for a somewhat sophisticated mulching technique.

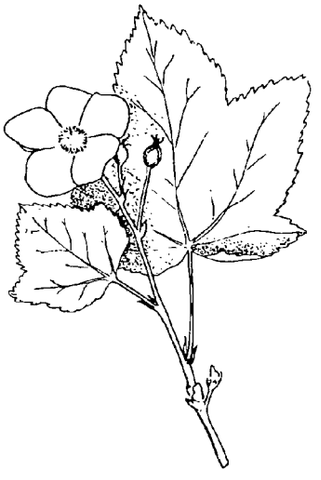
Most investigators conclude that the chief drawback to mulching is the cost. For example, Batchelder and Porterfield (1967) obtained higher yields of cotton from rows mulched with Soil Gard, but the yield increase was not sufficient to justify the cost, which was $82 to $138/ha. when applied in 25-cm. bands over rows 102 cm. apart. Likewise, Cannon (1966) emphasized cost reduction is essential to the success of synthetic strip mulches. He reported a cost of $86/ha. for petroleum mulch applied at the rate of 0.9 $m.^3$/ha. But he pointed out costs can be reduced through improvements in application techniques and lower costs of materials resulting from increased demand.

The concept of spot mulching, in conjunction with spot seeding, is worth considering as a way of reducing costs and as a practical technique. Liquid mulches effectively modified temperatures of 45-cm.-square seed spots in Canada (Fraser 1968). Many times, shrubs are needed most on terrain too rough to reach with mechanized equipment. A relatively small amount of mulch material, such as liquid applied from a backpack sprayer, could effectively conserve moisture and modify soil temperatures on a small, intensively prepared seed spot.

Based on trials at three field locations in Israel, Tadmor and others (1968) concluded that, although the economics of petroleum mulching may appear questionable, these one-time costs may be justified in light of the longtime benefits derived from a good stand of desirable plants on a given area, without the need of repeat seedings, weed control, and other extra measures.

Conclusions

The results of the research at Santa Fe, together with information from other investigations, suggest mulching should be considered for establishing shrubs in difficult environments. Both the natural and synthetic mulches offer possibilities. From the standpoint of ease of application, petroleum mulches offer considerable promise for modifying temperatures in the seed zone while at the same time conserving moisture. Certainly, broad opportunities exist for changing the degree of absorptivity and reflectivity through various additives. Finally, the whole subject of manipulating the microenvironment appears to be in its infancy.



Establishing shrubs in saline environments

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Attempts to grow salt-tolerant shrubs on saline soils date back to at least 1894 (McKee 1919; Morrison 1900; Nelson 1904). However, the methods previously used were haphazard, and plagued by failures. Nevertheless, Condon (1959), Smith and Malcolm (1959) and Plummer (1966), concluded that for reclamation purposes, saline areas should not only be protected and managed well, but plant species must be sown into these areas. Frith (1953) concluded that the usual agronomic techniques have to be profoundly modified to produce successful plantings on saline soils.

Soil factors affecting shrub establishment on saline sites

Salinity

There is ample evidence that the salt content of the soil and the hydrology of the site are the major factors affecting distribution of salt-tolerant plants on saline soils under natural rainfall conditions. However, because salts are so mobile in the soil, it is difficult to establish actual levels of salinity responsible for the presence of certain species or for particular establishment problems.

Levels of salinity in the soil associated with various species were reported by Branson, Miller, and McQueen (1967); Gates and Muirhead (1967); and Brown (1962). Salt levels in the soils of scalded areas in eastern Australia are reported by Beadle (1948d) and Jones (1969). The levels reported range from 0.062 to 4 percent total soluble salts.

There is a lack of appreciation in the literature for the significance of specific levels of salt in relation to the salt tolerance of halophytic shrubs at germination. Mayer and Poljakoff-Mayber (1963) found that a 50 percent reduction in germination of *Atriplex halimus* occurs at about 5.8 g./1. NaCl in the germination medium. If the effects of soil matric potential and of any inhibitors in the bracts of the seeds are ignored, then in a soil of 40 percent field capacity containing 0.23 percent total salts, a reduction of 50 percent could be expected in the germination of *Atriplex halimus*.

Salt content of soils varies greatly, depending upon the site and season (Jones 1969; Smith and Stoneman 1970). Moreover, the microtopography of the surface may greatly influence the salt content of the soil at the position of the seeds. Bernstein, MacKenzie, and Krantz (1955) demonstrated the importance of bed shape and placement of seed when irrigation was used; it is possible that careful design of bed shapes under natural rainfall could take advantage of these principles.

From these studies, it may be concluded that salts in the soil probably influence the establishment of shrubs. Furthermore, it is clear that consideration must be given not only to the amount of salt present but to the season in which it is sampled; to its variability, both horizontally and vertically in the soil and with microtopography; and to the duration of particular concentrations of salt in the soil.

Structure

Surface crusting of soils is reported by Williams (1960) and Koller, Tadmor, and Hillel (1958) to present serious problems for the establishment of *Atriplex* species. The effects of crusting include not only the prevention of seedling emergence but also reduction in infiltration of the water necessary for reducing salinity and allowing plant growth.

Poorly structured soils slake rapidly, thereby annulling the benefits of cultivation and furrowing (Condon 1960; Stannard and Condon 1958). Some of the adverse effects of poor soil structure on plant establishment have been related to aeration problems by Heydecker (1963).

Seedbed compaction has been used by Plummer, Christensen, and Monsen (1968) to improve establishment of plants on ranges. However, Tadmor, Hillel, and Cohen (1968) found that compacting the soil above seeds may seriously retard or prevent germination. The effects of artificial compaction at seeding time on the establishment of crops other than shrubs has been studied by Bowen (1966); Triplet and Tesar (1960); and Morton and Buchele (1960). In general, compaction of soil beneath the seed, pressing the seed into the compacted surface, and covering it with uncompacted soil appears to be the most satisfactory method of planting. The results are likely to be related to the period for which the water supply at the position of the seeds is optimum.

Water

On saline sites, water is necessary for shrub establishment, both for seed germination and to wash salt from the soil. Jones (1966a) observed that where water collects, plants grow and trap water which assists further establishment. He found that on reclaimed areas the soil stored an extra 6 inches of water as compared with scalded areas.

No critical work has been done on the effects of soil water matric potential on the germination and establishment of shrubs on saline soils. However, studies of other crops on nonsaline soils indicate that on the wet range, germination may be reduced, presumably because of poor aeration, and that at matric potentials lower than -10 atmospheres germination of most species ceases. Germination may be delayed at matric potentials below -1 atmosphere (Tadmor, Hillel, and Cohen 1968). The effects of matric potential are closely related to the effects of soil-seed contact and the ability of the particular soil to conduct water to the seeds.

Saline soils frequently have low infiltration rates. Beadle (1948b), Condon (1959), and Jones (1966b, 1969) all concluded that infiltration of water is a major factor in determining the establishment of plants. Consequently, methods of establishment that cause water to collect, or "pond," and thus ensure increased infiltration have given the best results. However, there is an associated problem in that established seedlings may be killed due to "ponding." Consequently, seeds should be placed either at or above the waterline.

Topography

Sloping sites are recognized by Stannard and Condon (1958) and Jones (1969) as unfavorable for establishment of plants on scalded soils. Water is shed from the sloping areas to the flats, where establishment is better. However, Malcolm (1961b) reported problems caused by shallow flooding in flat areas.

Aeration

Studies of the effect of aeration on the establishment of shrubs on saline soils are lacking. However, Bowen (1966) used aeration over a 7-day period as one criterion in an analysis of the factors affecting plant establishment in the field; and Tadmor, Hillel, and Cohen (1968) studied in detail the effects of soil aeration on the establishment of wheat and range grasses.

Texture

Tadmor, Hillel, and Cohen (1968) demonstrated that for different substrates there was a different characteristic of water supply to seeds. However, Springfield and Bell (1960) had previously failed to demonstrate a difference in establishment of *Atriplex canescens* on a sandy loam and a clay-loam soil.

Toxicity

Saline soils frequently contain high levels of exchangeable sodium, but the implications of this fact for halophytes have received little study. When Ashby and Beadle (1957) grew plants of two *Atriplex* species in nutrient solution with added sodium chloride or potassium chloride, they found that the plants were able to survive in soils having high levels of sodium but died when levels of potassium were high and levels of sodium were low.

Plant factors

Inhibitors and dormancy

Presence of either inhibitors or other dormancy mechanisms in halophytic shrubs has been demonstrated by many workers. Malcolm (1972) has published a detailed listing. Dormancy in halophytic shrubs results from such factors as a hard seed coat; sensitivity of seed coat to temperature, dryness, and light; and presence of water-soluble inhibitors in material surrounding the seed. The resulting requirements for satisfactory germination are probably a part of the mechanism by which each plant species has adapted to its particular environment. Nevertheless, these factors still present problems for establishment both by artificial means and for assisting natural regeneration. Methods used to overcome dormancy include: the removal of bracts enclosing the seed: scarification; dewinging; sulphuric acid treatment; cold treatment; and washing of water-soluble inhibitors out of the seed coats. Such treatments as milling have caused reduced germination and deformed seedlings.

Koller (1957) demonstrated a complex annual periodicity of germination in *A. dimorphostegia* in which germination fluctuates during the year from near zero to near 100 percent. Fluctuations occur in only one of the two types of seed produced by this species.

Treatments used to break dormancy frequently result in increased numbers of germinating seeds and also in greater speed of germination.

Seed quality

Beadle (1952) and Malcolm (1961a, 1964) found that harvesting of fully developed but unripened seed of *Atriplex, Kochia,* and *Arthrocnemum* spp. gave seed of good viability if it was air-dried following harvest. However, Golovchenko (1969) found that premature harvesting of *K. prostrata* should be avoided. Clarke and West (1969) found that date of collection and purity of stand influenced germination of *K. americana.* Various workers have found considerable differences in seed quality from accessions of seed of the same species collected from different sites.

In *Atriplex* species, harvested seed frequently contains apparently mature bracts without an enclosed embryo. Jones (1968) found for 10 harvested samples of *A. nummularia* that the amount of seed present ranged from 40 to 81 percent; its fill from 10 to 84 percent and its viability from 2 to 62 percent.

Russian workers (Strogonov 1962) found seeds obtained from plants grown on saline soil to be more satisfactory for planting on saline soils than seed that had grown on plants on nonsaline soil.

Maintenance of viability

Thoday, Tadros, and El Shishiny (1956) and Malcolm (1961a) found that seeds of *Kochia indica* and *K. brevifolia* lost viability rapidly when stored under room conditions. Cold temperatures and low humidity enable storage of the seed for longer periods. Seed of *K. sedifolia* retained viability for only a short time in the field (Specht 1960).

Williams (1963a), Springfield (1970), and Beadle (1952) found that seeds of *Atriplex* species usually may be stored for a few years without losing viability. Sometimes soft seeds of a species deteriorate but hard seeds retain viability. Seeds of the salt marsh plants, *Allenrolfea occidentalis* and *Arthrocnemum halocnemoides*, retain viability well (Gold 1939) and Malcolm (unpublished data). However, Horton, Mounts, and Kraft (1960) found that seed of *Tamarix pentandra* loses viability rapidly as does seed of *T. aphylla* (Waisel 1960).

Vigor, growth, and competition

The relations between seed size, speed of germination and emergence, vigor of root and shoot growth, and ability to establish and compete are closely interwoven. Such factors as weed growth, soil crusting, low rainfall, and salt accumulation militate against establishment of seedlings that germinate and grow slowly. The rate of germination of seeds of *A. nummularia* is believed by Jones (1968) to be a very important factor in determining its establishment on slaking soils. Even though Burbidge (1946) and Malcolm (1971a) have shown *Kochia* species to germinate very rapidly, establishment of *K. brevifolia* on saline soils is hazardous (Malcolm 1971b).

Nord and Whitacre (1957) obtained better germination from small seeds of *A. canescens* than from larger seeds; and although large seeds have a higher energy store, they also require more energy for emergence (Morton and Buchele 1960).

Whalley, McKell, and Green (1966) examined the germination and seedling vigor of range grasses and suggested that the processes were better understood if considered in three phases: heterotrophic, transition, and autotrophic. Efficiency of use of seed reserves, ability of roots to explore, and speed of germination were all factors that influenced seedling vigor. The relationship between the use of seed reserves, the emergence of the seedling, and the commencement of photosynthesis is important in establishment but has not been studied for halophytic plants. The principles explained by Asher and Ozanne (1966), Anslow (1962), and Lovell and Moore (1971) may be a helpful foundation for study of halophytic species.

Although detailed studies of seedlings of halophytic shrubs are lacking, several reports consider their ability to establish themselves against competition. Beadle (1948c) claimed that annual species provide protection for the establishment of perennials; but Koller, Tadmor, and Hillel (1958) and Knowles (1954) reported poor survival of *Atriplex* species because of competition from annual grasses; in addition, Jones (1966b) and Condon (1960) reported that establishment of *A. vesicaria* was depressed by sowing it with annual species instead of alone.

Salt tolerance

Berstein and Hayward (1958) concluded that normal crop plants are not more physiologically susceptible to salt at germination than later. However, Mayer and Poljakoff-Mayber (1963) working with *A. halimus* and Chatterton and McKell (1969) working with *A. polycarpa* have shown that these species were more sensitive to salt at germination than during subsequent growth. Results of germination studies by a number of workers on a wide range of halophytic species have been reviewed by Malcolm (1972). In general, the effect of salt on the germination of these species is similar to that on normal vegetable crops. A 50-percent reduction in germination occurs at about 5 to 20 g./1. NaCl, and germination is prevented at around 20 to 30 g./1. NaCl. Considerable differences in salt tolerance both at germination and in early seedling growth of accessions of the same species from different areas have been shown by Beadle (1952), Clarke and West (1969), Workman and West (1967), and Chatterton and McKell (1969).

Under natural conditions seed of halophytic species may lie either in or on saline soil for a considerable period before conditions become satisfactory for germination. Seeds of *K. indica*, *Salicornia rubra* and *K. brevifolia* have been shown by El Shishiny and Thoday (1953), Ungar, Hogan, and McClelland (1969) and Malcolm (1971a), respectively, to have the ability to maintain viability while standing in solutions highly saline for periods of a few days. Malcolm (1972a) found that viability of *K. brevifolia* dropped to about half over an 8-week period in moist saline soil.

Germination of some seeds under fresh conditions may be promoted by previously soaking the seeds in solutions that are highly saline (Clarke and Hannon 1970; and Malcolm 1971a).

The salt in the fruits or bracts surrounding the seeds of halophytes may be important. Beadle (1952) showed that the concentration of salt required to suppress the germination of some *Atriplex* species was lower than the concentration developed in fully absorbed bracteoles. Koller (1957) found that the seeds of *A. dimorphostegia* were hygroscopic. Perhaps when conditions are insufficiently wet for germination, the seeds are retained in an at-the-ready condition by the salt solution in the surrounding bracteoles; and when the salt is removed subsequently, germination may be completed in a very short time. If the mechanism operates as described, the implications of removing the bracts or washing the salt from them must be carefully considered.

Unfortunately, those studies on the effects of salinity on the germination and establishment of halophytic species have dealt with either the germination phase or with the established seedlings; but these studies have failed to follow the development of salt tolerance in the germinating seedling. Factors that assist the seedling in its transition from a highly salt-sensitive germinating seed to a highly salt-tolerant established seedling are among those vital for establishment.

The effects of salinity on germination of halophytic species are complicated by the interaction of salinity with temperature. Malcolm (1964 and 1971a) studying *Arthrocnemum halocnemoides* and *K. brevifolia*, and Rivers and Weber (1971) studying *Salicornia bigelovii* found that in the presence of salt the best germination occurred at the optimum temperature. At temperatures both above and below optimum, temperature and salinity interacted to give lower germination than would have been expected from either acting alone.

Water requirements

Seeds of some species of succulent halophytes and of *Tamarix pentandro* can germinate either when floating on water or when totally submerged (Clarke and Hannon

1970; Gold 1939; Horton, Mounts, and Kraft 1960). Germination of *K. indica, K. brevifolia,* and *Arthrocnemum halocnemoides* is satisfactory in shallow water (El Shishiny and Thoday 1953; Malcolm 1964 and 1971a). Burbidge (1946) found that three species of *Kochia* had a wide range of tolerance of saturation levels from 40 to 100 percent for optimum germination. By contrast, Beadle (1952) reported that at time of germination the seed of five *Atriplex* species must not be surrounded by films of water. However, submergence did not permanently damage the seeds. The mechanisms responsible for sensitivity to submergence in halophytic seeds have not been examined, but studies by Orphanos and Heydecker (1968) and Roos and Pollock (1971) are useful in clarifying the principles involved.

Although gas exchange is probably a major consideration for seeds in wet soil, as the soil becomes drier, stress effects are more important. Springfield (1968 and 1970) has shown that germination of *A. canescens* and *Eurotia lanata* is decreased and delayed by water stress, especially at high temperatures. Effects of presoaking seeds of halophytic shrubs prior to planting have been investigated by Frith (1953) for *A. semibacata;* Twitchell (1955) for *A. canescens*; and Jones (1968) for *A. nummularia*; all of these researchers discuss both the advantages and disadvantages of this procedure.

Toxicity

Gold (1939) found that seeds of *Allenrolfea occidentalis* burst but did not germinate in sodium carbonate solutions. A 10-percent solution of sodium sulphate prevented germination but did not damage the seeds unless seed coats had been scratched. He concluded that scratching permitted the entry of toxic ions.

Atriplex helimus grew better on a medium that contained equal parts of NaCl and KCl than on mediums composed of separate salt solutions (Mozafar, Goodin, and Oertli 1970). Greenway (1968) found halophyte growth to be adversely affected by solutions of calcium chloride but not sodium chloride at the same concentration. *A. polycarpa* was highly tolerant of boron in solution culture (Chatterton and others 1969).

Temperature requirements

The temperature requirements of halophytic shrubs range from those that are highly specific in their requirements for germination, such as *Arthrocnemum halocnemoides* var. *pterygosperma*, to various species of *Kochia*, which germinate through a wide range of temperatures. Temperatures lower than optimum normally cause slower and lower germination. Higher temperatures sometimes result in more rapid germination, but the final germination figures are lower than those obtained at the optimum. Both speed and total amount of germination are likely to be important in establishment.

Burbidge (1945) found that removing bracts from the seeds of *A. vesicaria* widened the range of temperatures that were satisfactory for germination. He also investigated the effects of high temperatures on seedling mortality. Both the duration and the frequency of periods of high temperature affected mortality. Malcolm (1971a) found that cold night temperatures delayed germination of *K. brevifolia.* However, for *A. halocnemoides*, Malcolm (1964) found that cold night temperatures, as a part of a fluctuating range, were required for germination. The interaction between temperature and water, salt, and inhibitors is discussed elsewhere.

Light requirement

All of the following workers concluded that light is of no consequence in the germination of these species: Beadle (1952) studying five *Atriplex* species; Koller, Tadmor, and Hillel (1958) studying *A. halimus*; Horton, Mounts, and Kraft (1960)

studying *Tamarix pentandra*; and Springfield (1970) studying *A. canescens*. However, Koller (1957) previously found that germination of *A. dimorphostegia* was almost completely inhibited by light at certain temperatures. Short periods of illumination actually stimulated germination. Sensitivity to light was lost when the coats of imbibed seeds were punctured, but germination of the punctured seeds was abnormal.

Aeration

Studies on the effect of aeration on seeds of various plants by Sedgley (1963); Grable and Danielson (1965); Orphanos and Heydecker (1968); Tadmor, Hillel, and Cohen (1968); and Roos and Pollock (1971) indicate that germination may be particularly influenced by even short periods of oxygen stress. However, Beadle (1952) using five *Atriplex* species and El Shishiny and Thoday (1953) using *K. indica* found that high concentrations of CO_2 had little or no effect on germination. Burbidge (1945) suggested that a poor supply of oxygen may be involved in the lower germination of *A. vesicaria* in bracts in wet soil.

Pathogens

Seedling mortality due to pathogens has not been reported in field studies on halophytic shrubs, but molds have been observed in germination studies in the laboratory. Mold growth was identified as a major factor influencing the establishment of *A. semibaccata* in a glasshouse study on salinized soil by Millington, Burvill, and Marsh (1951). Chaff obtained by dewinging seeds of *A. canescens* was found by Nord and Van Atta (1960) to cause faster mold growth during germination tests.

In germination studies on beetroot, Heydecker and Chetram (1971) found that microbial factors were not particularly important. Both fungi and bacteria were found on seeds, and the fungi produced antibacterial effects.

pH of germination medium

Beadle (1952) found that pH of the germination medium had no effect on five Australian *Atriplex* species. In the report by Gold (1939) on the toxicity of sodium carbonate to seeds of *Allenrolfea occidentalis*, pH may have been significant; or it may have been significant in the study by Malcolm (1971a) in which lime reduced the browning of root tips of *K. brevifolia* seedlings germinating in shallow water.

Adaptation

Because of the extreme hazards to establishment in saline areas, which are usually from arid to semiarid, it is important that shrubs should be carefully selected. First, they should be adapted as well as possible to establishing under the prevailing conditions. Second, they should be able to reestablish themselves naturally in order to ensure the long-term stability of the area. Third, they should be able either to live under the conditions prevailing or to bring about changes in the conditions so that cover is maintained or improved.

For scalded areas in New South Wales, Muirhead and Jones (1966) found that of a large variety of halophytic shrubs sown, only *A. vesicaria* persisted and spread on certain plots. Two annual saltbushes were reported by Condon (1959) to have colonized a wide variety of scalded soils in New South Wales. The value of annuals to improve soil condition was emphasized by Stannard and Condon (1958), who found that although plots sown to *A. vesicaria* alone failed, a good cover developed where annuals were included.

Climatic factors

In discussing problems of establishment on three degraded grasslands in Eastern Australia, Williams (1960) concluded that naturally occurring plants of *A. nummularia* and *A. vesicaria* may establish themselves in the best seasons, and that it may be hopeless to expect good results from plantings made in either average or poor seasons. Stannard and Condon (1958), Stannard (1962), and Malcolm (1969a) all emphasized the importance of climatic factors in the successful establishment of shrubs on saline or arid areas.

Temperature

Three distinct aspects of climatic temperatures are important in considering establishment problems: first, low temperatures, which may cause frost injury, or delayed or slow germination, or may assist in overcoming dormancy; second, high temperatures, which may destroy seeds or kill seedlings but may also assist in breaking dormancy or speeding germination; and third, duration of periods during which temperatures are optimum for germination and establishment.

After studying the temperature requirements of *A. vesicaria* and the temperature conditions following rainfall in the areas where it occurs in Eastern Australia, Burbidge (1945) concluded that temperatures rarely fall low enough for long enough periods to effect good germination and establishment. High soil temperatures in New Mexico were reported by Sosebee and Herbel (1969); they found that when shrubs were piled three deep to give sparse shading the soil temperatures were reduced by 21° C. In northern California, very short periods of optimum temperatures in spring for germination of *A. polycarpa* were found by Cornelius and Hylton (1969). For *K. brevifolia*, Malcolm found that the average terrestrial minimum temperatures in the wheatbelt were likely to delay germination.

Rainfall

Beadle's (1948d) observation that most scald reclamation must be done when there is natural rainfall has highlighted the crux of the problem of establishing shrubs on saline areas. In most areas where it is desirable to establish halophytic shrubs, rainfall is neither plentiful nor reliable. Moreover, rainfall frequently comes in the least convenient season for establishment, and its intensity and distribution are often not favorable. The amount and seasonal distribution of rainfall when temperatures are optimum determines the establishment of *A. canescens* (Springfield and Housley 1952). Important aspects of the effect of rainfall on establishment include: leaching of inhibitors from seeds (Koller 1955); and damage to the seed reserves in the soil (Burbidge 1945). Jones (1962 and 1966b) emphasized the relation of rainfall intensity and distribution to soil-crusting problems.

Beadle (1952) found that an inch of rain was sufficient to establish seedlings of five *Atriplex* species during winter. In his glasshouse trial, further rainfall resulted in larger seedlings but did not improve establishment. Malcolm (1971b) applied one-fourth, one-half, and three-fourths of an inch of artificial rainfall to glasshouse-planted seeds of *K. brevifolia*; after 25 days, the treatments contained zero, 13, and 41 seedlings, respectively.

Wind

Beadle (1948b) stated that wind-driven sand and and hot dry air cause cutting and desiccation of leaves. Cassady (1937) stated that wind blows seeds off barren areas, and Smith and Malcolm (1959) suggested that cereal rye be used to reduce sandblasting of *K. brevifolia* seedlings. Wind may blow water off flat sections of scalded land (Jones 1966a).

Evaporation

Evaporation levels for a 24-hour, hot summer day were given by Beadle (1948b) as 24.5 mm. for a scald area and 14.5 mm. for a nonscald area. Winter values were 9 and 4-1/2 mm., respectively. Higher evaporation rates reduced the opportunity for infiltration. On saline soils, evaporation at the surface causes accumulation of salts.

Time of planting

The planting methods used influence decisions on when to plant shrubs in salty soils. For example, if water is used in the planting operation, then a planting time can be chosen that coincides with optimum temperatures. If, on the other hand, some effort will be made to influence seedbed temperature (e.g., by the use of black mulch), then time of sowing could be arranged to more closely fit the water regime.

Springfield (1964) estimated spring and fall as the best times for sowing *A. canescens*; these choices were based on temperature studies. However, moisture was more plentiful in summer, and Springfield and Housley (1952) obtained best results in their field trials by planting in spring and midsummer. Cornelius and Burma selected early March (1970) as having temperatures best suited to establishment of *A. polycarpa*, and field tests confirmed this. For Western Australia, Teakle and Burvill (1945) suggested plowing in autumn to bury the salty soil crust and sowing after rain has leached salt down further. Matheson (1968) also recommended delaying sowing until salts had been washed out of the surface soil, but Condon mentions the hazards of bogging.

Modifying the environment for shrub establishment

Reducing soil salinity and improving water relations

The two basic requirements for satisfactory shrub establishment on salt-affected land are reduction of the salt content of soil and improvement of water supplies; these requirements are complementary. Many types of cultivation are used as well as mulches and conditioners, and the benefits that result from these techniques include better temperature regime, reduced soil crusting, and reduced wind blasting. The aims are usually the following: to ensure that water soaks into the soil where it falls; sometimes to concentrate water from other areas; to avoid waterlogging of seeds and seedlings; and to control salt and water movements in the soil so that conditions remain favorable long enough for establishment.

On shadscale areas in Nevada, Brown (1962) used cultivation methods, soil amendments, and mulch to improve establishment of grasses and browse. A half-inch sand mulch spread over rows of pubescent wheatgrass increased survival significantly but was the only successful treatment. Nevertheless, Beadle (1948) in New South Wales, Teakle and Burvill (1945) in Western Australia, and Tadmor (1964) in Israel have declared that cultivation is necessary to encourage water penetration and salt leaching; the trapping of seeds; and the reduction of erosion damage. Springfield (1963) emphasized the importance of careful seedbed preparation; he obtained much poorer stands of *A. canescens* on unprepared than on prepared seedbeds. The need for cultivation methods designed to increase water penetration has been emphasized by Anderson and Swanson (1949), Slayback and Cable (1970), Anderson and others (1957), Shamsutdinov and Korsun (1968), Beadle (1948d), Stannard and Condon (1958), and Condon (1960). Furrows and pits result in increased infiltration, trapped seed and sand, reduced wind velocity, and checked water flow. Deeper furrows and higher banks hold more water and retain their effect longer. Checkerboard furrow systems are recommended by Jones (1966b), who suggested further furrowing between the grids in later years. Jones (1967a) and Cunningham (1970) recommend the use of special ponding banks where scald soils have slopes of less than 1 percent.

The effect of cultivation, sand cover, and application of gypsum on seasonal salt movement in soil was studied by Smith and Stoneman (1970). Cultivation and sand mulch greatly increased downward salt movement during autumn and winter, but only sand mulch prevented the return of salt to the surface in spring. Gypsum gave no measurable effect.

In establishment experiments on *K. brevifolia*, Malcolm (1971b) obtained best results from the use of a mulch of grass clippings. For improving water penetration and retention, for reducing soil salinity and soil temperature, and for providing protection for seedlings, various surface mulches are recommended by the following authors: Cassady (1937; Marais and Bonsma (1941); Teakle and Burvill (1945); Beadle (1948d); Anderson and others (1957); Morton and Buchele (1960); Judd (1966); Matheson (1968); and Sosebee and Herbel (1969). However, Fleck (1967) found that grass mulch suppressed the establishment of *Puccinellia*, a grass, on saline areas; and straw mulch gave no benefit on shadscale areas in Nevada (Brown 1962). Oil mulch gave good results on noncracked cloddy soils (Tadmor, Hillel, and Cohen 1968). Gypsum may be used to improve establishment and growth, reduce soil crusting, lower salinity, improve soil water storage, improve calcium to sodium ratio of soluble salts and exchangeable ions, and reduce dispersion (Barley and Hutton (1956; Jones 1962, 1969; Williams 1960b, 1963b; Malcolm 1971b; and Newman, private communication).

The need to control excess water during winter has been reccognized in South Australia by Matheson (1968) and in Western Australia by Smith and Malcolm (1959). Using shallow W-shaped drains or small diversion banks to concentrate, divert, and control the surface water has been suggested.

Weed control

There appears to be conflict between the need to control competition while the delicate seedlings of perennials are being established, and the maintenance of a reasonable degree of cover on saline soils, which otherwise would be subject to wind and water erosion and degradation. Control of weeds either on a "strip" or "spot" basis may be successful in some areas. Problems of weed control were discussed by Plummer, Christensen, and Monsen (1968); Plummer and others (1955); Williams (1960b); and Goodin and McKell (1970).

Fertilizers

No response was obtained by Brown (1962) to the use of nitrogen and sulphur fertilizer on salt desert range in Nevada, but Williams (1963b) found that *A. nummularia* seedlings on two soil types benefited from both nitrogen and phosphate application. Five *Atriplex* species grown by Trumble (1932) on nonsaline soils in South Australia gave large responses to nitrogen fertilizer, and Clarke and Hannon (1970) improved the growth of salt marsh species under saline conditions by supplying nutrients.

Disease control

There are no reports of testing measures used for the prevention of damping-off in field sowings of halophytic shrubs. It is likely that the delays caused to establishment by high salt, low water, and soil crusting are likely to render the plants prone to disease.

Pest control

Plummer, Christensen, and Monsen (1968), Bridges (1941) and Nord (private communication) all reported rodent activity on plantings of halophytic shrubs. Anderson and others (1957) have recommended covering sown seed to prevent bird, rodent, or insect action. The author has noted heavy infestations of red-legged earth mite on young seedlings of *K. brevifolia*, and during summer, grasshoppers and Rutherglen bugs have been found on young bushes.

Grazing control

Grazing control is essential for success in establishment of halophytic shrubs on saline sites (Anderson and others 1957; Stannard and Condon 1958; Condon 1959; Smith and Malcolm 1959; Matheson 1968; and Malcolm 1969). Seedlings of salt-tolerant shrubs are frequently slow growing, and farmers may overlook them and allow damaging premature grazing. Stannard (1962) found that livestock hinder improvement of scald areas both during the wet and dry seasons. A period of 2 to 4 years' protection from livestock is recommended by Cassady (1937b) for plantings of *A. canescens;* and Marais and Bonsma (1941) recommended 2 years' protection for plantings of *A. nummularia* seedlings in South Africa.

Treating and planting the propagation material

Seed treatments

The advantages of dewinging seed of *A. canescens* listed by Springfield (1964) include faster germination, easier handling, less bulk, and easier soil coverage. It is not necessary, therefore, to justify this treatment except on the basis of better establishment. The effect of threshing seed of *K. brevifolia* was investigated by Malcolm (1971b) who found that poorer establishment resulted. Leaching of seeds offers no benefits other than improved establishment and, in fact, Jones (1968) failed to show any benefit in field sowings from leaching or milling of Oldman saltbush seeds.

Soaking the seeds of *A. halimus* for periods of up to 36 hours gave establishment benefits (Koller, Tadmor, and Hillel 1958). However, Frith (1953) and Strogonov (1962) have warned against planting soaked seeds in dry or highly saline soils. It is apparent that if seed treatments of any kind are used for establishing shrubs on saline soils, the full implications of the treatments and their relation to the method of sowing must be carefully studied.

Seed rate and placement

In view of the vagaries of the environment and the relatively small size of seeds of many halophytic shrubs, it is likely that precise placement of seeds is more important in arid and saline areas than it is for normal crops. Concrete recommendations are given by Makmudov (1966) and Shamsutdinov (1970) for seeding rates for halophytic shrubs. These are the only workers who have published precise recommendations; Smith and Malcolm (1959) recommend that *K. brevifolia* be sown at rates from a few ounces up to 2 pounds or more per acre; the eventual success possibly depends on natural dispersion from a few established plants.

Most studies conducted on depth of sowing for halophytic shrubs have indicated that the two methods preferred are either surface or very shallow sowing.

Field observations on shrub establishment on saline soils frequently show that best establishment occurs either at or near the waterline where it occurs in the furrows (Knowles 1954 and Jones 1967b). Jones (1967a) found that the growth of *Atriplex* was improved by sowing the seed either in furrows or cultivated strips in ponded areas. The use of ridging and the sowing of seeds on ridges are recommended, especially for waterlogged areas, by Matheson (1968).

Vegetative propagation

If the barriers to satisfactory seed establishment of shrubs prove insurmountable then either the planting of seedlings by mechanized methods or the planting of cuttings may be substituted. Detailed studies on the seedling establishment of *A. halimus* have been made by Tadmor (1964). Cultivation was beneficial to establishment, and when

there was favorable rainfall no supplementary irrigation was required. Good establishment of halophytic shrubs from seedlings on salty soils is also reported by Malcolm and Clarke (1971) and Jones (1967a).

Of the establishment of *Tamarix aphylla* Waisel's studies (1960, 1961), showed that cuttings rooted best in moist, light soil that was low in salinity. Growth of cuttings was markedly reduced by 0.1 and 0.2 molar NaCl; they were killed by 0.7 molar NaCl.

Conclusions

The complexities of shrub establishment on saline sites are so critical that it is a tribute to plant adaptability that any results have been achieved. The importance of interactions within the environment on establishment of seedlings must not be overlooked. In this review, interactions mentioned include those between: water and temperature; salt and temperature; speed of germination and crusting of soil; fertilizer and water supply; leaching of seed and retention of soil water; soil water content and aeration; water supply to seeds and compaction; gypsum and fertilizer; and season and salt content of the soil.

Not only are two-way interactions important for halophyte establishment, but such factors as fertilizer, soil matric potential, soil salinity, salt in the bracts of seed, gypsum amendment for crusting amelioration, and hydraulic conductivity of the soil may all operate and interact together on a seed in a soil. We must therefore recognize the importance of considering the whole situation in order to design satisfactory establishment methods. As a step towards designing successful establishment methods of saline sites, the following principles should be considered:

1. Find plants adapted to establishment and long-term growth on the planting sites.

2. Obtain good quality seeds that are well matured, carefully stored, and produced by plants of suitable genetic and environmental origin.

3. Apply methods of seed treatment that have been thoroughly field tested.

4. Prepare an adequate seedbed. Preparation will probably include cultivation and may include soil ameliorants to reduce salinity or toxic factors and crusting; it probably will include application of procedures to control insect pests and weeds.

5. Sow the seed at a predetermined rate and at a precise time in the season determined to be most satisfactory for establishment. The seed will probably be pressed into the soil and may or may not have a covering of loose soil on top as determined in field trials. Pay due regard to the needs of both germination and survival in relation to the rainfall events most likely to occur.

6. Apply beneficial treatments such as fertilizer, cover crop, soil amendment, and mulch as applicable. The use of expensive treatments such as grass mulch may be justified as spot treatments.

7. Consider using supplementary irrigation and seed soaking.

8. Control flooding and wind erosion, if necessary,

9. Control insects, rodents, and grazing animals, as applicable.

There are gaps in the knowledge required to apply these principles, but at least if they are followed most of the factors operating will have been taken into account. The possibility remains that the mechanized planting of seedlings may be the most satisfactory method for establishing halophytic shrubs in saline areas.

Demonstration of a new shrub seeding method

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Throughout the period from 1956 to 1963, I was responsible for the range-improvement planting of more than one million saltbush seedlings in the Negev area.

At first the planting was done manually by relief labor. Then, in 1961 I adapted a disc plough, and thereafter the planting was done semimechanically.

Although the results were good, it became apparent that saltbush could become a real mainstay of range improvement only if a cheap and easy method could be found for its propagation.

The good rainfall year of 1963-1964 produced an abundance of voluntary seeding which permitted a great deal of observation on the conditions necessary for good germination and establishment. A quest through world literature on the subject did not show any successful seeder in existence. The Hansen browse seeder developed in Utah in 1964 has been improved so that it now performs acceptably even on rough terrain.

The reports by Burbidge (1945) on *Atriplex vesiccarium*, and Springfield and Bell (1967) on *A. canescens* confirm that the best seedling emergence was obtained when seed was placed at depths ranging from one-half to 1 inch. Similar results were obtained by Riedl and others (1964) and by Statler (1967) with *Eurotia lanata*. Using *A. nummularia*, Jones (1968) showed that seed germination was not the limiting factor in field-sowing failures. Seeding in spots improved the chances of emergence and survival according to Ferguson and Basile (1967), who worked with bitterbrush (*Purshia tridentata*).

My experience in the plant nursery indicated that 14 days is the time necessary for general seedling emergence. Therefore, it follows that the soil contacting the seeds should have a favorable moisture content for this 14-day period.

Hodgkinson and Rogers (1970) found that 14 days after seeding of *A. nummularia* and other *Atriplex* spp. in summer, the root depth reached 20 cm., and thereafter grew at a rate of 5 cm. per day. Again, my own experience with nursery-raised seedlings has taught me the supreme importance of deep stirring of the soil. The differences in soil-stirring depths often determine whether success or failure occurs. Sometimes deep stirring results in plants three times as large as those growing in a noncultivated field.

Depth of moisture necessary for survival of planted seedlings was found to be 50 cm. This can be obtained in most years by concentrating the runoff along strips that are ploughed on the contour prior to planting. Glendening (1939) showed the importance of shading the ground to retard the drying of surface soil. McGinnies (1959) found that this effect can be obtained at the bottom of a deep furrow.

Observation of volunteer seedlings showed that an abundant emergence of seedlings is necessary for a survival rate sufficient for a full stand. Although a denser stand may sometimes be desired, 700 to 1,000 mature plants per hectare can be considered a full stand.

A seeding implement

A seeding implement that provided some of the essential conditions described in the applicable literature was developed and has been used in the Negev Desert, Israel; it was demonstrated at this Symposium.

This implement consists of a rigid tyne furrow opener that produces a furrow about 15 cm. deep; a revolving drum with an adjustable aperture that drops abundant seed in spots along the furrow, about 120 cm. apart; and a large V-shaped wheel that presses the seed into the moist soil and leaves the furrow in a proper shape. The seeds then lie either near or on the bottom of the furrow between the surface and the 2-cm. depth. The implement is mounted on a three-point linkage general purpose tool carrier for use on a wheel or crawler tractor.

Small-scale trials of the planting method were conducted in the winter of 1969-1970, and the implement was modified and reconstructed in 1970. A full-scale field trial carried out in the winter of 1970-1971, using *Atriplex halimus* as the test species, produced completely successful results. This complete success was originally thought to be due to both the lower evaporation rate from the bottom of the furrow and to collection of additional runoff water from the furrow slopes.

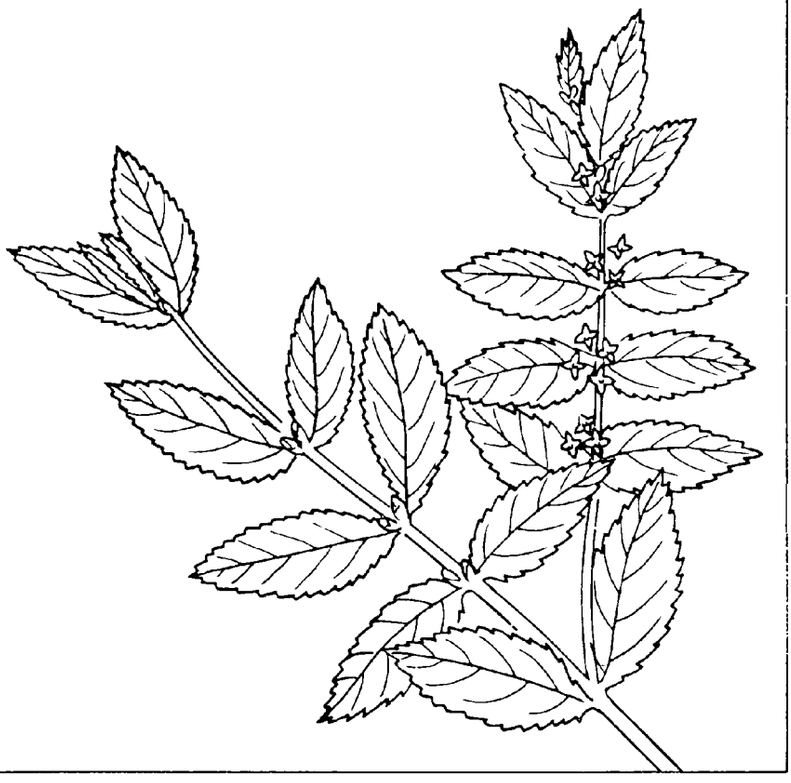
During trials of this seeder it was observed that surface soil in the bottom of a furrow was often moist in the morning even though the surface soil all around was dry. D. Hillel[1] pointed out that "It is possible for water to move within the soil from under the ridges to the bottom of the furrow in response to thermal gradients which occur as a result of the differential warming of the soil. That is to say, soil water can move in both liquid and vapor forms from the warmer ridges to the cooler furrow-bottoms. This movement can help to sustain the seedling during its critical establishment stage." Thus, the seedling can draw on reserves of moisture and, within practical limits, deeper furrows will provide increased moisture reserves. In areas subject to intense rainfall, the furrow bottoms may not be the best location for placement of seeds because flooding may occur there.

The author hopes that this method will be useful in areas having cultivable soils but where recurrent droughts make cultivation impossible or too risky. Another possible use for it would be the establishment of low, shrubby windbreaks in grain fields.

[1]Personal communication.

Section VIII.

The Future of Shrubs in Arid Lands



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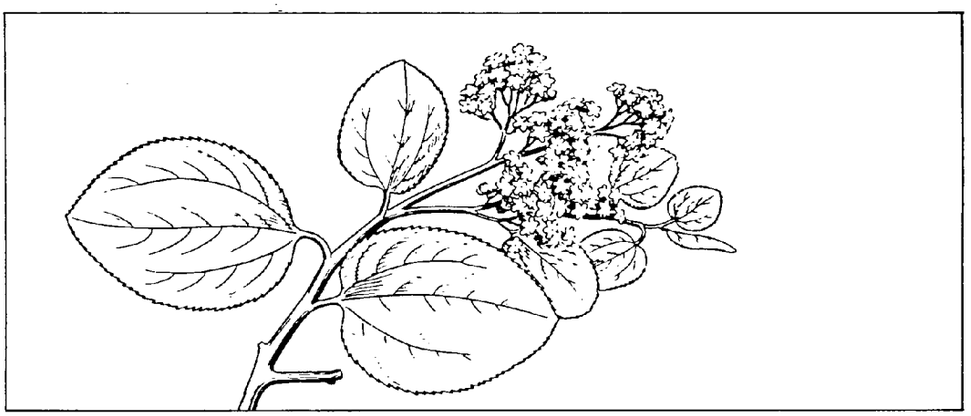

Needs and opportunities for shrub research in the Western United States

James P. Blaisdell

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Shrubs are a very important group of plants in the West, where they are natural components of major vegetation communities. They provide food and cover for wildlife and livestock, contribute to natural beauty of landscapes, furnish screening on recreational areas, and are useful for stabilizing soil on eroding watersheds and sites disturbed by road construction, mining, or other activities. Although their importance was recognized many years ago (Van Dersal 1938), they have never been adequately studied.

Because of their value as browse for big game and livestock, particularly on winter ranges, much of the limited research accorded to shrubs has been related to their use by browsing animals. Studies dealing with ecology and management of salt-desert shrub communities in southwestern Utah (Hutchings and Stewart 1953) and revegetation for improvement of big game winter ranges in southern Idaho (Holmgren and Basile 1959) and central Utah (Plummer and others 1968) are examples. Much of our knowledge of native shrubs in the Western United States, then, is in the areas of response to grazing, palatability and nutritive value, reaction to such environmental factors as climate and fire, and methods of propagation. I think it is fair to say that this symposium has effectively identified and assembled most of the available information. If a particular subject has not been discussed, you can rather safely assume a dearth of knowledge.

Research needs

In view of the many present and potential uses and values of shrubs, a sound knowledge base is needed to allow effective management of native shrub communities, development of superior shrubs for a wide variety of uses, and successful propagation in numerous ecological situations. Inasmuch as there are so many unknowns connected with shrubs, almost any kind of research will contribute new information. Perhaps the most important research needs will fit into the following categories: synecology of natural shrub communities, autecology and physiology, revegetation of disturbed areas, and genetic improvement toward development of superior shrubs.

Synecology

Considerable information on characteristics and functioning of natural shrub communities has been developed, particularly by range scientists concerned with management of the forage resource. Past attention has been focused on vegetation and its reaction to utilization by grazing animals (Hutchings 1954; Pechanec and Stewart 1949; Reynolds 1959), but some consideration has also been given to effects of such factors as precipitation and fire (Blaisdell 1953 and 1958).

However, much additional ecological information is needed to provide satisfactory answers to a number of practical questions: What shrubs are undesirable in what situations? How can undesirables be controlled? What is the best mix of shrubs with other kinds of vegetation for achieving particular management objectives? What are the interrelations of wildlife and livestock use?

Despite their seemingly simple nature, shrub communities are often variable and complex with innumerable combinations of biotic and abiotic factors, many of which have been largely ignored. Scarcely anything is known about diseases and insects or their impacts on vegetation. Not enough attention has been given to soil and soil organisms. Small mammals and birds, and their effects, have been given only limited study. Although some attention has been given to effects of precipitation on shrub communities, scarcely anything is known about effects of other climatic factors.

These components are closely related and function as an ecosystem, which includes flow of energy and transformation, circulation, and accumulation of matter through the medium of living organisms and natural physical processes. Integrated research by multidisciplinary teams will be necessary to develop a more complete understanding of the various shrub ecosystems. Of particular importance are the interrelations of the various components and the effects of manipulating them through management on the functioning of the natural system. The approach developed by the Desert Biome group of the U.S. International Biological Program--process studies to develop functional expressions, computer modeling, validation studies for checking computer models--seems to have particular promise. However, much research will be required before we can hope for a complete understanding of whole ecosystems.

Autecology and physiology

Although considerable information has been developed for certain shrubs, particularly ornamentals, the total accumulation of ecological knowledge for individual wildland shrubs is rather meager. However, fairly complete life histories have been made for a few species--such as budsage *(Artemisia spinescens)*, bitterbrush *(Purshia tridentata)*, western snowberry *(Symphoricarpos occidentalis)*, red elderberry *(Sambucus racemosa)*, fourwing saltbush *(Atriplex canescens)*, and winterfat *(Eurotia lanata)* (Wood 1966; Nord 1965; Pelton 1953; Conrad and McDonough 1972; Plummer and others 1966; Riedl and others 1964).

As evidenced by presentations at this symposium, numerous physiological studies have been made of various species, especially in such areas as drought and salt tolerance, nutrition, and response to clipping. However, in relation to total needs, there is little physiological information on wild shrubs.

As a basis for further study and for immediate use in management, research is needed to determine characteristics and requirements of numerous species. For example, more information is needed on seed germination, seedling establishment, survival, growth, and seed production; optimum and tolerable ranges of moisture, temperature, nutrients, light, soil reaction, and other environmental factors; efficiency in utilizing moisture; compatibility with other vegetation; and resistance to defoliation, trampling, and other impacts of use. This research should draw on studies in other fields such as range, forestry, horticulture, landscaping, etc.

Revegetation

Much research attention has been given to the rehabilitation of depleted rangewatersheds throughout the West. Since the mid-1930's, Forest and Range Experiment Stations of the Forest Service, the Agricultural Research Service, State Agricultural Experiment Stations, and Universities have developed reliable guides on equipment and

methods for seeding, proper season, local adaptation of species, and subsequent management of seeded stands. This has allowed successful seeding of several million acres throughout the West. Unfortunately, the emphasis was on grasses; only a little attention was given to forbs and almost none to shrubs.

Revegetation research in connection with improvement of wildlife habitat, particularly big game winter range, has properly been concentrated on shrubs, and considerable information is now available (Plummer and others 1968). For example, cooperative efforts of the Intermountain Forest and Range Experiment Station with the Utah Division of Wildlife Resources and the Idaho Department of Fish and Game have screened hundreds of shrub species, and some 75 have been identified as promising for revegetation of big game winter ranges and other disturbed sites in the West. Two particularly good native shrubs for this purpose are big sagebrush *(Artemisia tridentata)* and rubber rabbitbrush *(Chrysothamnus nauseosus)*. Both are rather easy to establish, are highly productive, and grow well in mixtures with grasses and forbs. Others that have been singled out for their desirable characteristics are fourwing saltbush *(Atriplex canescens)*, antelope bitterbrush *(Purshia tridentata)*, desert bitterbrush *(P. gladulosa)*, cliffrose *(Cowania stansburiana)*, black sagebrush *(Artemisia nova)*, Mormon tea *(Ephedra viridis)*, winterfat *(Eurotia lanata)*, golden currant *(Ribes aureum)*, snowberry *(Symphoricarpos oreophilus)*, serviceberry *(Amelanchier utahensis)*, and honeysuckle *(Lonicera tatarica)*. Some information is also available on site selection, season for planting, and methods to use.

It is readily apparent, however, that much more information is needed to allow establishment and maintenance of shrubs in a wide variety of situations, including ranges primarily used for livestock grazing. Of particular importance is revegetation of road cuts and fills, areas disturbed by mining operations, and other depleted areas where soil fertility and stabilization are serious problems. In addition to identification of adapted species, development of special equipment and methods for revegetation of these harsh sites seem to require a major research effort. Although some research has been undertaken (Plummer 1970), it is only a beginning.

Another important need, which is basic to revegetation efforts, is information on seed technology and nursery practices for the production of seedlings. Methods should be developed for producing and harvesting seed from shrub stands established for this purpose, for processing seed to facilitate handling or to break dormancy and increase germination, and for proper storage to maintain viability. Likewise, nursery practices should be developed to allow quantity production of shrub seedlings and transplants for situations where direct seeding does not produce satisfactory results.

Development of superior shrubs

Scarcely any work has been done on genetic improvement of wildland shrubs. However, preliminary investigations have revealed considerable variation among natural populations in regard to such characteristics as germination and growth habits, growth rate and productivity, palatability and nutritional values, disease resistance, insect susceptibility, and drought, cold, and fire tolerance. Once we understand the range and especially the genecological significance of local and geographic variations, we can use this knowledge to assure good adaptation in seeding and planting ventures. Next we can develop superior stock through intense selection within native races, by racial or species hybridization, and by other means. The magnitude of potential improvement is indicated by what is being accomplished with agricultural crops.

Research opportunities and plans

Because of the wide variety of potential uses for and the lack of information about wildland shrubs, opportunities for productive research are very great. Although one of the first recognized uses of shrubs was for game and livestock forage, stabilization on road cuts and fills, mine dumps, and other badly disturbed areas may be an even more

important use for shrubs. Likewise, screening on recreation areas and beautification of various landscapes are also potentially important uses. Agencies such as the Bureau of Land Management, Forest Service, Soil Conservation Service, Bureau of Reclamation, Federal Highway Administration, State Highway Departments, State Land Departments, and the State Fish and Game Departments have need for information about shrubs and can be expected to lend their support. Likewise, interest and support are anticipated from many private companies, societies, conservation organizations, and individuals.

The Intermountain Forest and Range Experiment Station of the Forest Service has developed plans for a major shrub research program to be headquartered in Provo, Utah, on a site provided by Brigham Young University. Funds for planning the Shrub Improvement Laboratory were appropriated by Congress in FY 1967, and architectural and engineering specifications are now complete. Research funds were provided in FY 1972, and a research program is already underway.

Plant materials are now being assembled from a wide variety of sources, so that promising species, ecotypes, and strains can be evaluated for various characteristics pertinent to use on wildlands over a wide range of environmental conditions. Selected native plants will be tested in nurseries and outplantings on variable yet representative sites in Utah, Idaho, Oregon, and Nevada, in cooperation with fish and game departments and other State agencies. In addition, shrub introductions for similar testing will be sought through the New Crops Research Branch of the Agricultural Research Service, the National Seed Storage Laboratory, the Soil Conservation Service, State Agricultural Experiment Stations, and through AID, FAO, or other contacts in foreign countries.

Although considerable progress should be possible through selection and testing, breeding programs will eventually be necessary to combine outstanding traits from selected individuals. Accordingly, cytologic, genetic, and reproductive traits will be studied and appropriate breeding programs will be undertaken. Hopefully, some of the necessary research will be conducted by such institutions as Brigham Young University, utilizing their special talents and facilities.

Research on seed technology and nursery practices will lean heavily on background information from related agricultural, horticultural, and forestry fields. Available facilities and technical expertise from Utah State University Agricultural Experiment Station will be utilized through proffered cooperation on seed production, progeny testing, and nursery operations. Additional assistance will be sought from National Forest nurseries, the Soil Conservation Service, the Nevada Division of Forestry, or other organizations.

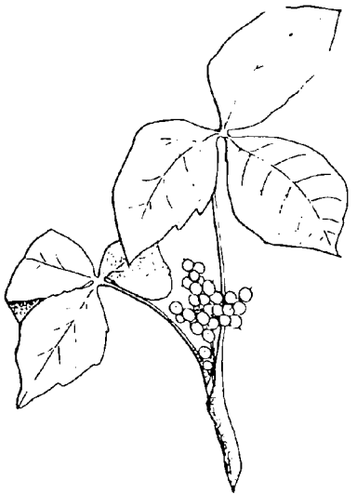
In the Intermountain Station, shrub revegetation research will be continued at the Shrub Improvement Laboratory and will also be included in the program of wildlife habitat, watershed, and recreation research units. Past results will be refined and extended to additional ecological situations, with emphasis on the Great Basin and other intermountain areas. The developmental phase of this effort will be highly cooperative with fish and game departments and land management agencies. Extension to such uses as screening on recreation areas, soil stabilization on roadsides or mine dumps, and beautification of landscapes will require assistance from state highway departments, the mining industry, recreational interests, and others.

In addition to certain autecological and physiological studies at the Shrub Improvement Laboratory, synecological studies of the various shrub communities will be provided by research units assigned to develop management practices. For example, range research units at the Intermountain Station have been assigned ecology and management of sagebrush-grass, salt-desert shrub, pinyon-juniper, and mountain brush. The effect of fire on shrubs is being studied at numerous locations. Considerable attention is being given to selection and testing of fire-resistant shrubs for use in high-hazard areas at the Forest Fire Laboratory of the Pacific Southwest Forest and Range Experiment Station.

Because of the interest recently expressed in wildland shrubs and their uses (this symposium is just one example), it seems that much progress will be possible if available research resources are utilized in a coordinated effort. The Shrub Improvement Laboratory of the Intermountain Station will serve as a coordinating unit for shrub research programs of the Forest Service in the four western Forest and Range Experiment Stations. Since a number of State agencies are actively cooperating in the present research program of these Stations, considerable coordination will be automatically achieved. I am not suggesting that the Shrub Improvement Laboratory serve as a coordinating unit for other research efforts; however, review of Laboratory programs and progress might be helpful to those contemplating shrub research of their own.

Perhaps now is a good time to say something about policy. The Forest Service encourages cooperation, and any authorized research of the Forest Service may be done in cooperation with others. It can include exchange, use, or sharing of information, materials, equipment, personnel, funds, and facilities. Cooperation stretches the research dollar, strengthens research programs of cooperating institutions, develops mutual understanding and confidence, and facilitates dissemination of results and getting scientific knowledge into practice. I believe it safe to say that it is possible to develop satisfactory cooperative arrangements for any reasonable proposal. One point of my own philosophy: I think we should attempt to obtain personal involvement in cooperative research and make it more than the usual exchange of funds.

We have important needs and excellent opportunities for progress--if we utilize available talents, facilities, and funds in cooperative and fully coordinated research. Certainly this is a real challenge.



The role of shrubs and shrub ecosystems in present and future Mediterranean land use

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The object of this paper is to point out the role that shrub ecosystems and individual shrubs should play in the solution of some pressing problems of Mediterranean land use. These problems arise from the rapidly growing demands on open lands for urban expansion, outdoor recreation and tourism, clashing with the need for increased production of food, forage, and pasture from nonarable mountainous regions.

Israel can serve as a good example for this discussion. It is at the southeastern corner of the Mediterranean Sea and is bordered by arid and semiarid desert and steppe zones; it embraces a wide range of environments. These include the UNESCO (1963) thermo-Mediterranean and xerothermo-Mediterranean bioclimatic regions that have typical Mediterranean sclerophyll tree and shrub vegetation, to which most of this discussion is devoted.

Israel is already beset with the severe dilemma that all other nations in this region will soon face: its nonarable Mediterranean wildlands are threatened both by urban sprawl and despoliation and by increasing pastoral and agricultural pressure from a rapidly growing population. But, at the same time, it will be increasingly important to preserve the open, unspoiled nature and attractiveness of these wildlands for the growing needs of urban population and tourism, so they can serve as a "landscape therapeutic" countermeasure against the monotony and stresses of modern urban life in the industrial society.

Ecology of Mediterranean shrublands

In Israel, as in other Mediterranean countries, the only true wildlands still dominated by natural sclerophyll woody vegetation are located in mountainous regions having annual rainfall of more than 400 mm.; they have soils too steep, too shallow, or too rocky to be cultivable (fig. 1). These wildlands comprise about 40,000 ha., or 40 percent of the total area of North and Central Israel (Seligman and others 1959), and similar proportions in other Mediterranean countries (Tisdale 1967).

Walter (1968) recently summarized present knowledge about the ecology of this "duriligneous" vegetation and concluded that the Mediterranean region is comprised of innumerable variants of different degradation and regeneration types. Most current information about the ecology of this vegetation in Israel has been derived from extensive studies made chiefly by the Department of Botany at Hebrew University, Jerusalem, by Zohary and his colleagues (Zohary 1962). Eig (1927) was the first to subdivide these sclerophyll vegetation types into forests and "maqui" if dominated by trees, "garigue" if dominated by shrubs up to 1 m. in height, and "batha" (a biblical term) if dominated by a mixture of dwarfshrubs, hemicryptophytes, geophytes, and therophytes. Whereas most of the sclerophyllous, hardwood species, like *Quercus calliprinos, Q. ithaburensis, Pistacia palaestina, P. lentiscus,* and *Phyllirea media,* have very low economic value for timber, the herbaceous understory contains a profusion of beautiful flowering geophytes and many valuable pasture grasses and legumes.

Figure 1.--Nonarable mountain shrubland in Israel.

During a history of human intervention lasting through more than 10,000 years, the original Pleistocene climax forests have turned into human degrades and converted upland ecosystems. This landscape desiccation has recently been described by Naveh and Dan (1971) as anthropogenic biofunctions corresponding to the main phases of changing land use throughout history. One of their main conclusions, derived from study of recent biofunctions, was that during the long phase of agricultural decay and population decline in the last hundreds of years a new equilibrium has been established on those noncultivated upland ecosystems that are neither overgrazed and heavily coppiced nor completely protected. This man-maintained equilibrium between trees, shrubs, herbs, grasses, and geophytes has contributed much to the biological diversity and attractiveness of the Mediterranean landscape and is, without doubt, one of its main assets for recreation and tourism. This is true not only for Israel, but also for other eastern Mediterranean countries like Greece (Knapp 1965). However, in the last 20 years, this equilibrium has been increasingly distorted by radical changes in land use resulting from mechanized land reclamation and cultivation; also by increasing pressure from large beef cattle and milk sheep herds around Jewish settlements, overstocking by goats and cattle around Arab villages, combined with patch cultivation on nonterraced slopes after rootgrubbing of shrubs, and, above all, the rapid processes of urbanization and water and road development, which now reach even the remotest mountain villages. Agnostopolous (1967) pointed out a similar situation in Greece.

Of considerable impact on the mountainous landscape in Israel and in other Mediterranean countries having similar afforestation programs is the planting of monospecies pine forests, chiefly *Pinus halepensis*, carried out in Israel with great efficiency by the Jewish National Fund on an area of some 40,000 ha. More than half of these forests are considered only as protection forests, and on much of the remaining planted area, potentials for timber production are low. Much effort has been spent in recent years on development of recreation amenities and picnic areas in these forests, but their recreation value is restricted mainly to the forest edges because the plantings are dense and monotonous and lack a herbaceous understory and wildlife.

One important result of the constant defoliation of the maqui scrub vegetation, grazing, cutting, and coppicing, was the selection of species and biotypes that have better adaptation to the desiccated habitats and have greater resilience and regenerative powers. Outstanding in these qualities are such trees and shrubs as *Quercus calliprinos*,

Ceratonia siliqua, Pistacia lentiscus, Phyllirea media and many others, which combine resistance to summer drought with resistance to frequent burning, browsing, and cutting. This resistance is achieved by a deep and extensive root system, a scleromorphic leaf structure, a hydrostatic water economy (Walter 1968), and by great regenerative powers from roots and dormant buds (Naveh 1960).

Of great ecologic significance for the stability of these shrub ecosystems is their capacity to provide effective protection to the soil and to restore its fertility by a dense, strong root network and a great amount of leaf litter and mulch, which accumulates beneath the dense canopy of foliage. The organic matter content of the upper 4-cm. layer of a shallow, brown rendzina soil on rocky, shrub-covered slopes in Western Galilee amounted to 16.3 percent under *Quercus calliprinos*, 19.3 percent under *Pistacia lentiscus*, and 20.8 percent under *Ceratonia siliqua*.

Even after this organic matter had been reduced by about a fifth by burning, more than 10 percent organic carbon was retained in the whole soil profile, and 13 to 16 percent in the upper layer. This and the excellent granular structure and high infiltration capacity of these maqui soils may explain why even after denudation by fire, no runoff or soil movement could be detected after heavy early winter rainstorms on slopes up to 40 percent (Naveh 1960).

The role of goats in traditional utilization of Mediterranean shrubland

In response to the special ecological and socioeconomic conditions of these mountainous, rugged, shrub-covered regions, a distinct animal husbandry has developed in which the ranging black Mamber goat is important. It is well adapted to the meager seasonal forage, to scarce water supply and the rocky terrain, and can take best advantage of the prevalence of sclerophyll and thorny shrubs for producing milk, meat, and hair. French (1970) pointed out that goats are the most efficient converters of fiber-rich, lignified plants and that they can consume daily as much as 8 percent of their live weight in dry matter as compared with 3 percent or less consumption by cattle and sheep.

In observations on feeding habits of ranging Arab cattle and goats, Naveh (1960) found that on brush ranges in Western Galilee, goats regularly ate 30 of 40 common woody species. Cattle, by contrast, utilized only about 10 woody plants--chiefly trees--during the dry season and after brush fire.

In a year-round study of a typical Arab black goat herd in Upper Galilee, Weitz (1964) estimated that goats spent about two-thirds of their grazing time on woody plants in mixed *Quercus calliprinos, Pistacia palaestina* maqui, and *Poterium spinosum* batha. Each hectare provided 500 grazing days or 400 Scandinavian Feed Units per annum. In winter and spring all the milk was left for the kids, but from April to September the average lactation per goat was 87 liters and a net profit of 40 IL.[1] was derived from each goat (3.5 IL. = $1). In comparable conditions in Greece, net annual profit per goat is around 150 drachmas (30 drachmas = $1) (F.A.O. 1964).

The income derived from this shrubland in Israel by goat browsing was about four times higher than that estimated in the Israel Range Survey (Seligman and others 1959) for utilization of such brush ranges by cattle. It is comparable to the average output of annual grassland hill pastures in this region.

Because of these economic advantages from utilization of Mediterranean scrub by goats, it is not astonishing that the comparative density of goat population to human population in these countries is the highest in the world, namely, 1:2.6 as compared with the world average of 1:8.9 (French 1970). Goat populations have decreased in most countries during recent years, but goats are still numerous in Turkey (some

[1] Israeli pounds.

19 million, or 7 percent of the world's goat population); 6 million in Morocco; 4,866,000 in Greece (with a stocking rate of 3.84 goats/ha. of scrubland); 630,000 in Syria, 500,000 in Tunisia, 400,000 in Lebanon (ranging freely on 85 percent of the whole territory), 162,000 in Cyprus, and 105,000 in Israel (of these, 70,000 are range goats).

In spite of low milk yields (less than 70 liters per nanny), goats are important in the economy of these mountainous regions. In Cyprus, for instance, milk, meat, skin, and hair from goats make up 34 percent of the gross animal husbandry product and 7 percent of the agricultural product; in Greece, goat milk provides one-sixth of the total animal husbandry and 63 percent of the total family income in mountain regions; and in Lebanon they provide livelihood for 25,000 persons, and 40 percent of the population directly depends on goats for milk and meat.

However, as this Symposium has stressed, because of poor management of livestock and grazing, the present production of these goats is not only very low, but their impact on the land, in combination with uncontrolled grazing by cattle and sheep, is disastrous. This was confirmed by Tisdale (1967) in a survey of Mediterranean countries; he found most Mediterranean and semiarid rangelands severely deteriorated and undergoing accelerated erosion. The situation is worsened by demands for increased agricultural production from submarginal and from steep, nonterraced and patch-cultivated slopes, combined with the clearing and rootgrubbing of shrubs and over-exploitation of the remainder for fuel and fodder (Naveh and Dan 1971).

Range goats can survive and produce on land not fit for cattle and sheeep (fig. 2); so they have been blamed as the main agent of Mediterranean land ruin. But they are really only the last link in a vicious chain of land devastation brought on by indiscriminate burning, cutting, grazing, and slope denudation and cultivation. French (1970) accurately stated that the Mediterranean goat problem has been distorted by emotional reactions and misconception. These led to the conclusion that the only way open for rational land use is a complete ban on goats and the reclamation of Mediterranean uplands as closed forest vegetation--either by encouragement of natural revegetation or by afforestation to which goats, without doubt, are most harmful. He stated: "It is typical of the irrational condemnation of goats that these animals are blamed for

Figure 2.--This small herd of black goats is on typical shrubland unfit for grazing by cattle and sheep.

initiating and accelerating soil erosion whereas they may be only one of the factors involved. They are not even an integral part of this destructive chain because severe erosive damage can and does occur in their complete absence. The crop cultivation of agriculturalists certainly plays a bigger role in initiating and perpetuating erosion damage than do goats...The belief that goats and soil erosion are always associated is thus unfounded."

"Neither," wrote French, "is there any direct, inevitable relationship between the density of livestock in an area and the amount of soil erosion which occurs there. The erosive losses are more related to the soil type and often, as in the Peleponnesus area of Greece, there is no evidence that the presence of goats and sheep exert any direct effects. Instead of blaming the goat for all the errors of man, and especially for denuding the natural vegetation and depleting the soil fertility to the point where other domestic livestock can no longer secure a living, efforts should be concentrated on an assessment of the true value of goats in the various national economies and the grazing needs of other livestock."

Such an unbiased reassessment was attempted in the F.A.O. Goat Symposium in 1964, which recommended that instead of closing all untillable and rocky shrublands from goat grazing and denying rural populations an important source of income, efforts should be made to find better and more profitable systems of goat husbandry and of controlled grazing and improved range management for a sustained yield. Full advantage should be taken of the potentials of browsing goats to produce milk, meat, mohair, and skin without having adverse effects on rangeland, forest, and watersheds.

Dynamic and integrated planning and management of Mediterranean upland ecosystems

Naveh (1968, 1970) recently discussed the problems of nature conservation and of multiple use of Mediterranean upland ecosystems for pasture, forest, recreation, and watershed management. He warned of the fallacy of regarding their complete protection and their conversion into unpenetrable, biologically depleted natural maqui "protection" or planted "production" forests as the only alternative to present misuses and deterioration. Instead, he proposed enlightened approaches of dynamic and integrated ecosystem planning and management, in which their functional and structural diversity could be conserved and their biological productivity increased. Management should be aimed at optimization of landscape values and of their "noneconomic richnesses" and environmental qualities and, at the same time, at derivation of greater economic benefits from multiple uses for recreation, tourism, wildlife habitat, milk, meat, and hair production, and increased water yields, according to ecological site potentials and socioeconomic needs.

For this purpose he suggested subdividing nonarable Mediterranean upland ecosystems into three main land use and problem areas:

Nature Reserves

Here, the main aim of scientific management is the conservation of biological diversity by a flexible dynamic conservation policy, also proposed by Moerzer-Bruijns in Israel (1969). Destructive disturbances, such as overgrazing and mass recreation, should be avoided; but three main levels of controlled intervention should be adopted, namely:

a. Continuation of "conventional" defoliation activities, including moderate goat grazing and occasional fires and confinement of "modern" disturbances and activities to prescribed restricted areas and walking paths provided with buffer zones as large as possible.

b. Preservation of considerable portions of representative ecotypes and landscape units for complete protection as control and study areas.

c. Reservation of other representative areas to experimental manipulations and ecosystem studies on long-term effects of grazing, cutting, trampling, burning, spraying, and other disturbances.

Nature Parks and Recreation Areas

The chief aim here would be the optimization of landscape values to enable maximum enjoyment by visitors with minimal damage to natural resources. Creation of densely planted fire-prone monotonous and one-aged pine forests or unaccessible maqui thickets minimizes these values. On the other hand, these values would be maximized by active stimulation of biological diversity through integrated ecosystem management for the conversion of maqui, garigue, and batha into open forests, woodlands, and savannas and by creation of edge habitats and favorable niches for a rich, flowering carpet and for wildlife.

Remaining Uplands

In these, the chief aim would be economic utilization for direct benefit of rural populations. Dynamic planning and management of multiple use patterns would be required. These should be based on scientific ecosystem methods, on cost/benefit ratios, and on simulation and optimization to make best use of natural resources on a sustained yield base and on advanced agro-ecological and biochemical technologies as described below.

Unfortunately, present knowledge is not sufficient to provide objective and quantitative parameters for such dynamic multiple use planning and management. Therefore, comprehensive ecosystem studies are urgently required on: (1) the structure, function, dynamics, and productivity of these nonarable upland ecosystems; (2) their response to different management practices; and (3) their ecological, hydrologic, and socioeconomic implications and constraints.

We can now discuss only generally a few of the options open for such multiple uses on which experience has been gained in Israel and point to other alternatives, which have not yet been tried.

a. *Conversion of closed maqui into open tree-shrub-grass savanna pastures.*--One of the first requirements for rational use and for increase in landscape values and yields of forage and water is the opening of dense and closed maqui, garigue, and batha and converting them into productive and attractive, multilayered seminatural savannas covered by desirable trees, shrubs, grasses, and herbs.

In Israel as in California (Sampson 1944; Biswell 1954; Sampson and Jespersen 1963), controlled burning has been found to be the cheapest and most efficient means to open dense brush stands and to enable further integrated management and improvement (Naveh 1960; S.C.D. 1964).

Controlled burning of dense stands of sclerophyll woody species (e.g., *Quercus calliprinos, Phyllirea media, Pistacia lentiscus, P. palaestina)* provides an ideal seedbed for locally growing and for reseeded perennial grasses such as *Oryzopsis miliacea, Phalaris tuberosa.* It also encourages germination and spreading of many flowering geophytes from the Liliaceae, Iridaceae, and Orchidaceae families, which have been suppressed, together with the above-mentioned perennial grasses, by the dense brush canopy and by lack of light (Naveh 1960; Loeb 1961; Diskin and Naveh 1971). Because these brown rendzina and terra-rossa maqui-soils have high infiltration capacity, runoff and erosion from fire-denuded slopes are negligible even in the first winter after burning. Well developed and desirable fodder and ornamental trees, such as *Ceratonia siliqua* (Carob) and *Cercis siliquastrum*, can be protected by firebreaks. The regeneration of undesirable thorny and unpalatable shrubs and dwarfshrubs can be prevented by selective spraying with 2-4,D and 2-4-5,T (Naveh 1960). In more recent trials, Tordon

101 has been most promising for arboricidal control of these plants, and its use will make spraying cheaper and much easier (Cohen, Daniel and Weitz 1969).

Although more than 200 grazing days/ha. and more than 1,000 Scandinavian Feed Units/ha. per annum for mature beef cattle could be obtained from converted maqui scrub, the need for hand labor and for high initial investments (300 to 400 IL./ha.) have been prohibitive for large-scale conversion. In garigue and batha thickets, which have low potential value, the probable success of reseeding with perennial grasses is very low and the danger of accelerated erosion after fire is much greater. Here, burning stimulates germination of dwarfshrub seedlings. Most of these dwarfshrub species, especially *Poterium spinosum* and *Callycotome villosa*, are most sensitive to foliage spray with 2-4,D; consequently, conversions, based on air sprays and on rotational-deferred grazing in fenced ranges, are much cheaper, amounting to 100 IL./ha. and can therefore be effected on a larger scale (Naveh and Ron 1966).

b. *Using fire and goats in integrated ecosystem management.*--Shantz (1949) reviewed the use of fire in Mediterranean land management and concluded that it can be very useful but also very dangerous, especially if used indiscriminately in combination with grazing and cutting. Unfortunately fire has been used unwisely sometimes in the Mediterranean region; consequently, its use has been condemned altogether. Such wholesale condemnation should be replaced by a balanced objective reassessment of its appropriate place in the scientific management and utilization of Mediterranean uplands. Before any definite recommendation can be made regarding its practical value in integrated multiple use in different ecological and socioeconomic sets, much more information should be gathered on its role in the release and recirculation of nutrients now bound up in the lignified woody brush cover and litter. Attention should also be paid to its possible role in stimulation of germination and development of desirable geophytes and pasture plants and in the removal of phytotoxic kolines accumulating in unburned litter and duff.

The same holds true for goats. Not only are they the most efficient domestic converters of woody plants into animal products, but they can suppress sprouting shrubs after fire, cutting, and coppicing; they could be used as a cheap biological tool to follow up after burning and mechanical and chemical treatments for brush control.

Our grazing studies in burned maqui and garigue in Western Galilee showed that grazing goats and cattle inflict greatest damage to resprouting woody plants and to indigenous and reseeded perennial grasses in the first winter after the fire. Grazing them also encourages less palatable, thorny and aromatic species, especially *Salvia*, *Cistus*, and *Rhamnus*, and increases the hazards of soil erosion (Naveh 1960). In later years, goat browsing hampers the regrowth of trees, especially of such palatable species as *Pistacia palaestina* and *Ceratonia siliqua*, until they reach a stem height of about 2 m., when their twigs are out of reach. From this stage on, controlled goat browsing can be most useful in suppressing woody understory and root sprouts. This has been demonstrated in recent large-scale conversions of closed maqui of *Quercus calliprinos* and *Pistacia palaestina* in Western Galilee into open recreation forest; this has been carried out by the Jewish National Fund, Forest Department. In this conversion, the brush thicket was opened by hand clearing and coppicing for charcoal.

Without doubt, the crucial and most difficult problem in goat ranging is the enforcement of control on grazing in space and time. Adequate control can be achieved only as part of a comprehensive program for an overall rise in productivity of livestock to an economically profitable level.

In my opinion, rational use of nonarable rangelands, including improved shrub ranges on a sustained yield base, can be ensured only in fenced paddocks and pastures in which stocking rates, grazing intensity, and timing can be adjusted to range condition, carrying capacity, and improvement objectives.

Experience in Israel with range management and improvement of Mediterranean uplands during the last 20 years has shown thattalthough fences alone do not ensure proper management, they are its first and indispensable tool. However, fencing and improvement are feasible only if sufficiently high profit can be ensured from such improved brush ranges, which could serve as economic motivations and justify initial investments. Such profit can be achieved only by a modernization of the traditional goat husbandry. Laor stated (1967) that the existing milchgoat husbandry could be improved by better housing, veterinary care, feeding, and by crib feeding of kids with cheap milk substitutes. In this way, milk yields of 200 liter per goat could be achieved; this milk could then be processed into high quality cheese for local market and export. This would assure a net profit of 80 IL. per nanny and could also pay for range improvements.

Another possibility, suggested by Laor and Barnea (1970), is to confine milk production to sedentary stable fed and high quality Saanen goats, which have proved highly successful in Israel, and to use shrubland ranges only for meat production of black goats, which should be kept exclusively on fenced brush ranges. They calculated that a herd of 10,000 local black goats kept on 400 ha. could produce a net income of 32.23 IL. per goat. Fencing and range facilities would require initial investment of 6,000 IL./ha.

A first practical attempt for controlled goat grazing in fenced brush ranges in Israel was made by the collective settlement called "Jodphat" in Lower Galilee with improved Angora goats. These goats were introduced by Naveh (1962) from the Edwards Plateau in southwest Texas[2] because of their success in a modern profitable farm-ranching system in rocky, shrub-covered, fenced pastures that resemble goat range in Galilee. Unfortunately, because of lack of manpower, this project was not properly concluded, despite its promising early outcome. Nevertheless it has yielded important information.

The Angora goats from Texas, far superior to the original Turkish stock in mohair and meat production, adapted themselves easily to the new environment of a typical Mediterranean hill farm in Israel. For almost 3 years, except for a few rainy and cold winter days, they and their kids were maintained in fenced maqui scrub dominated by *Quercus calliprinos* and *Pistacia lentiscus*. Stocking rates were light to moderate, and the annual requirement of 300 Scandinavian Feed Units per goat could be provided by about 0.6 ha. of shrubland. Additional 30 Feed Units were given by supplemented stall feeding. Later the Angora goats were herded together with Hawassi milk sheep, and their diet consisted of a well balanced mixture of grasses, herbs, and shrubs. A most important advantage these Texas goats have over the local agile black goats is their quiet temperament and their adjustment to being kept without supervision in regular 4-wire fences. Mohair and meat production were very similar to those obtained from a well managed herd in Texas: they reached an average weight of 20 kg. after 1 year and about 40 kg. at maturity; mohair yields were 5 to 8 kg. By crossing Angoras with local black goats, heterosis induced considerably higher meat yields but reduced the quality of mohair. The milder winter and spring climate and the lush, green fodder at that season in Israel ensured conditions more favorable to early shearing than those in Texas. Using prices in 1966 as a basis for calculations, an economic unit of 400 she-goats, 400 kids, and 10 he-goats could ensure a net income of 63 IL. per goat and 62 IL. per working day and a net profit of 76 IL./ha. of fenced shrub range. Investments for fencing, water-points, etc., would have amounted to about 100 IL./ha. as compared to 220 IL. that is necessary for intensive brush conversion for cattle.

Economic prospects for Angora goat raising depend very much on world market prices for mohair, but the possibility of achieving higher yields of goat meat by crossbreeding.

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[2]Thanks are due to Mr. Perry Kallison, San Antonio, Texas, and to Dr. L. B. Merrill from Texas A&M College, who were very helpful in this project.

can also ensure a better balanced business enterprise. These possibilities should be studied carefully in different sets of ecological and socioeconomic conditions. However, in order to avoid failures similar to those encountered in this scheme, the systematic introduction of highest quality healthy stock from Texas, South Africa, or elsewhere, should not be carried out as a commercial enterprise but as a scientific research project. Sufficient funds should be available not only for importing a large enough number of goats to enable handling of the mohair, but also for scientific investigations of the goats and pastures and for veterinary care.

New methods of Mediterranean shrubland utilization in multiple use

Heavy expenditure required for conversion of closed maqui and socioeconomic constraints of strict control and of sophisticated management practices necessary for shrub range utilization on a productive, sustained yield basis, will limit their large-scale applications. Fenced-off shrub ranges will considerably limit their multiple use benefit for recreation and tourism, to which highest priority will frequently be given. Therefore, other nonconventional alternative ways for the conversion of primary productivity of woody sclerophyll vegetation into animal products should be investigated. One of these, which deserves attention and study, is the possibility of encouraging browing gazelles and other ungulates and birds for game and sport hunting by opening of closed maqui on selected sites; this could be accomplished through burning, chemical brush control, water development, and salting, in combination with restocking and other management practices that have proved effective in comparable ecological conditions in California (Sampson, Jespersen 1963).

A different method of shrub utilization could be based on the traditional Zager system of forage forests, practiced in the Karst of Dalmatia in Yugoslavia. In this system, branches of trees and shrubs are lopped and stall-fed in the winter to cattle and goats. Ziani (1965) proposed the development of improved utilization of branch fodder by machine-chopping and milling of branches, twigs, stems, and leaves and by ensilation with molasses. The palatability and nutritional value of many hitherto useless woody plants might be increased by pelleting this chopped fodder together with concentrates and molasses. Experience gained by the California Division of Forestry in chopping, milling, and pelleting of stems, twigs, and leaves of Ceanothus shrubs, similar in size, appearance, and leafiness to *Pistacia lentiscus* (Naveh 1968), could greatly benefit this study.

Exploration of possibilities of brush chopping techniques should not be limited to the production of livestock fodder but should include consideration of new biochemical technologies for development of vitamin- and protein-rich food and industrial products. If selective mechanical chopping of shrubs were applied properly, it might become an efficient means for creating favorable niches for ornamental flowers and for wildlife in open recreation forests, without resorting to use of fire and goat grazing, which can become disastrous if permitted to run out of control.

Development of feasible mechanical methods of collecting, handling, and economically utilizing sclerophyll trees and shrubs could completely change the present outlook of land planners, foresters, and decision makers who regard maqui scrub more as a menace than an asset. Raising the economic potentials of these brushfields would enable additional inputs, which are essential for halting present misuse and neglect of Mediterranean upland ecosystems. It might open the way for better nature conservation and for the integration of the "noneconomic richness" of biological diversity and landscape values with the derivation of direct economic benefit from the shrubs, the increase in water yield, and the recreational land potentials.

For the future of shrubland ecosystems in Mediterranean land use, it will be most important that the response of shrubs to mechanical defoliation and the economical utilization of chopped and pelleted brush fodder and other possibilities be investigated.

The role of fodder shrubs in the improvement of open Mediterranean hill land pastures

Great areas of nonarable Mediterranean upland are open grasslands and degraded batha, in which sclerophyll plants have only minor importance. Systematic studies, followed by commercial farm operations, have shown that moderate stocking and rotational-deferred grazing of fenced hill land pastures could double initial output (Seligman and others 1959). With additional intensive improvement and integrated ecosystem management through NP fertilizing, selective spot spray of weeds, perennial thistles, and thorny shrubs, production from these lands could be even trebled, and more than 1,000 Scandinavian Feed Units per ha. could be achieved. Although investments for fencing and improvements range between 50 and 100 IL./ha., forage production costs from such intensively managed and fenced pastures are lower than those in unfenced, degraded ranges and amount to less than one-third the cost of any other fodder produced on the farm (Naveh and Ron 1966; Naveh 1970b).

In spite of this increase in pasture output, intensive ecosystem management has not overcome the main limitation of animal production from these annual ranges; namely, its dependence on seasonal and annual fluctuation between the wet and dry season and between favorable and less favorable growth seasons.

This climatically induced fluctuation was demonstrated in the results of a 6-year grazing trial in a typical annual hill land pasture in Lower Galilee, where average annual rainfall is 550 mm. (table 1). Although the coefficient of variation in annual rainfall was only 23 percent, that of forage production was 65.6 percent in the unfertilized and 77 percent in the fertilized pasture. The amplitude in forage yields between the wettest and driest year ranged between 300 and 400 percent, respectively, and that of meat production between 370 and 400 percent. Because of the poorer quality of the dried-off forage, very little live-weight gains could be attained in the dry season, and these only by supplementing with one-half kg. of protein-rich concentrates. At that season 2 to 3 times more rangeland per head was needed than in the spring.

Multiple regression analyses between bimonthly rainfall, minimum December-January temperatures, and annual pasture output revealed also the high correlation between these limiting climatic factors and productivity, which was even increased by fertilizing (Naveh and Lumas 1971).

It is therefore obvious that even by intensive agro-ecological management and improvement the chief bottleneck in Mediterranean pasture production could not be removed. As it will be progressively more difficult to devote scarce land and water resources to production of livestock fodder instead of to food and high income cash crops, the importance of the remaining nonarable, open pastures for livestock production will grow, and all ecological and economically feasible means should be found to raise its productivity. For this purpose, drought-resistant, succulent, or summergreen (palatable) and highly productive fodder shrubs, which can produce lush nutritious fodder in the dry season and serve as emergency fodder in drought years may be most valuable. Such plants are used already in other semiarid regions, especially in Australia, South Africa, and Brazil, but they have proved themselves also in semiarid Mediterranean conditions in North Africa. According to Le Houerou (1970), yields of 30 to 50 metric tons of spineless cactus and 1,000 to 2,000 Scandinavian Feed Units per ha. of *Atriplex halimus* have been obtained chiefly in the dry season, in regions that receive 250 to 300 mm. annual winter rainfall.

Also in Israel, plants like *Atriplex halimus, A. nummularia, A. canescens, Kochia brevifolia, Cassia sturtii, Acacia cyanophylla* etc., are showing much promise in preliminary grazing trials in semiarid conditions of the Northern Negev with 200 to 300 mm. annual rainfall (Forti 1970; Karmon 1968).

Table 1.--*Variation in productivity of intensively managed herbaceous upland pasture ecosystem in Lower Galilee, based on grazing trials Nve Yaar 1953-1959 (Average annual rainfall, 550 mm.)*

Productivity measures	Unfertilized pasture			Fertilized pasture		
	Total	Green	Dry	Total	Green	Dry
Forage production (dry matter, g./m.^{2})						
Average for 6 years		240.2			363.5	
Maximum (wet year)		448.0			844.5	
Minimum (dry year)		110.0			131.4	
Coefficient of variation (percent)		65.6			77.1	
Meat production (kg./ha.)						
Average for 6 years	105	94	11	194	159	36
Maximum (wet year)	213	173	40	317	235	87
Minimum (dry year)	46	46	0	62	62	0
Coefficient of variation (percent)	55.5			44.2		
Pasture output (Scandinavian Feed Units/ha.						
Average for 6 years	73	61	12	120	95	25
Maximum (wet year)	136	109	22	175	136	46
Minimum (dry year)	44	33	0	62	42	7
Coefficient of variation (percent)	45.9			29.9		
Pasture requirement (per head/month/0.10 ha.)						
Average for 6 years		2.6	5.2		1.9	4.8
Maximum (dry year)		4.0	10.3		3.0	3.1
Minimum (wet year)		1.6	3.4		1.4	2.0

There is no reason why these and other shrubs could not be established in marginal fields and open pastures in the same way as Allepo pine seedlings. The aim should be to create seminatural pasture savannas, composed of a therophytic layer of productive grasses and legumes and a phanerophytic layer of productive fodder shrubs and trees, to increase ecological diversity and energy and nutrient tapping by the vegetation canopy. Spacing of the planted or directly sown shrubs should be wide enough to minimize competition for light, water, and nutrients and, like the indigenous xerophytic woody vegetation, these plants should be able to utilize deeper soil pockets, rock layers, and crevices.

Continued provision of green fodder should be emphasized rather than short-seasoned provision of edible fruit and pods, as is the case with carob trees and *Acacia albida*. These are available only during shorter periods and if consumed in the pasture in too great quantities they might cause digestive disturbances and have only limited nutritive value.

Experimental work along these lines has already started, independently in two semiarid countries with Mediterranean climates--Chile and Israel. In both, much effort had been spent previously on the establishment of perennial grasses in marginal and dryland pastures, until it was realized that this will not solve the above-described, crucial problems of fluctuability and unreliability in forage supply throughout the year from natural and dryland herbaceous pastures.

In Chile, this work was started in 1959 by the Faculty of Agriculture and Forestry Science, University of Chile, Santiago, and has already proceeded far enough to point out a number of local and introduced species that are most promising and deserve more intensive study and propagation in actual grazing conditions. Among these are such local shrubs as *Atriplex repanda, A. coquimbana, A. atacamensis, Fuchsia lysioides, Carica chilensis, Bridgesia incisaefolia, Oxalis gigantea, Caesalpinea angulicaulis, Adesmia arorea, A. cinerea, Baccharis racemosa, Chenopodium paniculatum,* and among the introduced, outstanding are *Atriplex nummularia, A. semibaccata, A. canescens*, and *Kochia brevifolia.*

Systematic experimenting on fodder shrubs and trees, chiefly material that showed promise at the Desert Research Institute in Beer Sheba, has started only recently, although Naveh tried experimental field planting of spineless cactus as early as 1944 and Berlinger followed (1965).

In 1969, the Soil Conservation Division began field plantings of fodder shrubs and trees in terra-rossa soil pockets on rocky, nonarable terrain in Upper Galilee which was earmarked for pine-forest plantations; some of these plants, especially *Acacia horrida, A. ciliata, A. nerifolia, Cytisus procifera, Dodonea viscosa,* and *Cassia sturtii,* have shown outstanding early development and growth (Elan 1969). Systematic evaluation of numerous fodder shrubs is now carried out in typical subhumid Mediterranean conditions at the Acre Experimental Station. Additional work is carried out in cooperation with the Soil Conservation Division in drier and warmer conditions in the Bet Shan Valley. Some outstanding shrubs, such as *Atriplex nummularia, A. canescens* spp. *linearis, A. glauca, Cassia sturtii,* and *Medicago arborea,* have been planted this spring in replicated field conditions of a degraded batha on shallow and rocky pale rendzina soil near an Arabic village, Macher, near Acre. The planting of 6- to 12-month-old seedlings and the maintenance of the shrubs have used the same methods as those used in Allepo pine afforestation by the Jewish National Fund, Forestry Department; this agency is willing to expand multiple purpose fodder, cover, and ornamental shrub "afforestation" on a larger scale (fig. 3). This will be very important because in this way the long-term experience of foresters in establishing and growing woody plants in difficult environments and in rocky and shallow upland soils will be available and will promote its success.

However, much more extensive research will be needed to solve the problems of selection, establishment, and utilization of these shrubs.

Because this work is so important and its scope is so broad, it should be carried out as an international project in closest cooperation with teams of ecologists, physiologists, foresters, and specialists in animal husbandry. Experience gained in other semiarid regions will be most beneficial, but the special conditions of the Mediterranean mountainous region, the problems of shallow soils on soft or hard limestone of basalt, heavy competition of winter growing herbaceous plants and the adaptation of management systems suitable to the various patterns of farming and livestock husbandry can be solved only in local setting.

Figure 3.--Experimental area for shrub propagation administered by the Jewish National Fund.

Importance of shrubs and their ecosystems for vegetation engineering and derelict land reclamation

The open Mediterranean landscape and its structural, visual, and functional continuity are threatened not only by increasing pressure for additional agricultural and pasture land but also by rapid urbanization and industrialization. Rapidly growing populations demand more and more land and water for this expansion, and thereby enforce more drastic and far-reaching changes on the open landscape than any agricultural and pastoral economy has previously done. Powerful bulldozers and other earthmoving equipment have razed the living sponge of forests, shrubs, and grasslands. They are replaced by buildings, installations, asphalt highways and stone-and-concrete bedded waterways and pipelines. All these are devoid of the absorptive powers of the original vegetation canopy; they are visible by ugly wounds of denuded slopes and embankments and abandoned quarries that increase the hazards of flooding, soil erosion, and environmental pollution over wide areas and thus spoil the landscape.

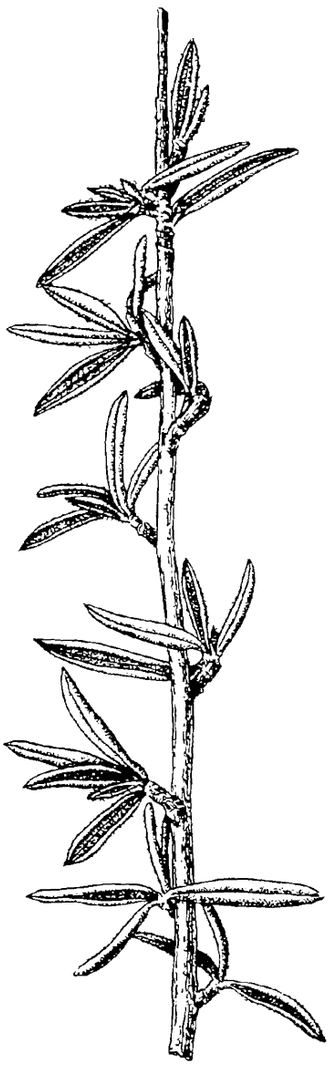
In Mediterranean and other semiarid countries, the dangers of man-induced wind and water erosion are especially severe, particularly on sandy, friable, erosive soils; and in rugged, steep country also, the processes of natural revegetation and recovery are slow. In Israel such damage is most conspicuous in the densely populated Coastal Plains, where intensive agriculture and water resource development is coupled with rapid urban sprawl, industrial expansion, and highway construction. But its impact on the landscape is most severe in the scenic mountainous regions.

In order to heal these neotechnological "civilization wounds," to stabilize and protect denuded slopes, cuts, and fills of highway embankments, bridges, and engineering installations, and to rehabilitate these human-degraded landscapes, special methods of ecological protection must be applied. In these, the capacity of grasses, shrubs, and trees should be utilized to act as powerful mechanical barriers, to reduce the kinetic energy and impact of moving water, sand, soil, and stones to serve as biological filters and sponges for the absorption of water, pollutants, dust, and noise, and to create stable and attractive ecosystems with their environment.

These possibilities have been recognized in many technologically advanced countries, and a new science called "vegetation engineering" has evolved, in which ecologists, agronomists, foresters, landscape planners and architects and engineers pool their efforts to find suitable plant material and cheap, mechanical ways for establishing and maintaining them in diverse, man-created habitats (Knabe 1965; Stark 1966). In Israel, some effort has been spent to develop similar vegetation-engineering methods for the biological stabilization of moving sand in the Coastal Region, around buildings and along roads and highways, and for stabilization of waterways and drainage canals (Naveh and Elan 1970). Promising beginnings have also been made in landscape reclamation of denuded slopes and along highways, and mechanical methods have been developed for the preparation of these slopes (Kalvariski 1969) for hydroseeding and mulching (Morin 1969). Systematic studies have commenced on the application of a dynamic ecosystem approach. This differs from both the phytosociological European approach to vegetation engineering, which emphasizes ecological reconstruction of potential, natural vegetation along highways with the exclusion of exotic plants, and from the pragmatic agronomistic and landscape architecture approach. In this, the choice of species is merely a matter of convenience and is based on pasture-grass mixtures and ornamental garden plants without reference to their surroundings. Out aim is to establish in these manmade habitats, seminatural, multistructured, and stable communities chiefly of indigenous, but also introduced hardy and drought-resistant herbaceous and woody plants that can maintain and reproduce themselves without irrigation and with minimum care (Naveh 1969, 1970b).

The most important source of plants for this purpose are our indigenous xerophytic phanerophytes, lithophytes, and chamaephytes. These are well adapted to the harsh physical environment of dry, calcareous, rocky, exposed slopes and can efficiently use solar energy, the limited moisture and nutrients, for foliage and root growth and also for the biological enrichment and physicochemical improvement of the poor soil and rock substrate through accumulation of organic matter, from leaf litter and duff. *Pistacia lentiscus* is a model for the biological, ecological, and mechanical features required. Plants chosen for vegetation engineering and landscape beautification should also be able to establish themselves quickly, preferably by direct seeding with the aid of hydromulching and of rapid development of a dense, compact foliage canopy, and a strong and extensive root net. Plants selected for landscape beautification should be distinguished also by such ornamental features as lively colors and conspicuous flowers and should maintain their attractive appearance through the dry season without irrigation and horticultural care. Good examples for these features are some of the aromatic Labiatae--such as *Rosmarinus, Lavendula, Xantholina, Salvia,* and *Cistus*--and also introduced drought-resistant shrubs like *Eriocephallus africanus,* which shows much promise in our early evaluation. Shrubs planted along highways should not be inflammable, as *Poterium spinosum* is, and should be resistant to air pollution from car exhausts, and especially to nitrogen oxidants, PAN, ozone, and others. No single "miracle shrub" combines all these desirable features; for each ecological and engineering environment, suitable mixtures must be devised. These should include ornamental perennial pioneer grasses, such as *Oryzopsis milacea, Pennisetum aspergifolium,* and legumes (chiefly annual clovers and medics, such as *Trifolium clypeatum* and *Medicago polymorpha);* these should be combined with the most desirable and attractive taller and persistent woody species. In this way a condensed and controlled seminatural process of secondary succession and revegetation should be accomplished.

At the same time, attention should be given to development of suitable mechanical methods of seeding and mulching with efficient organic and synthetic substrates, integration of biological and mechanical devices for soil erosion control and insurance of a better establishment and stabilization, even in steep slopes. Work on these lines has commenced in Israel and it is hoped that other Mediterranean countries will follow it very soon with much more extensive studies. Their object should be to find practical ways to utilize the inherent efficiency of natural and seminatural Mediterranean shrub ecosystems to be ecological buffers against environmental pollution and dereliction and to help minimize the detrimental impact of technology on the quality of our environment and life.



Manipulating shrub - grass plant communities in arid zones for increased animal production

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Lands devoted to grazing by domestic animals in northern Mexico occupy nearly 100 million hectares (247,100,000 acres). Although most are classified as desertic, arid, or semiarid zones (CFAN-CID 1965), these lands provide some of the most nutritious and palatable species of forage plants. In these regions, a prosperous, extensive livestock industry makes an important contribution to the national economy. Over 8 million head of cattle, 2 million sheep and goats, 1 million horses and mules, and many million head of wild animals depend on the vegetation of these arid zones.

Ecological characteristics vary within these 100 million hectares (247,100,000 acres); although large areas are occupied by pure, open grasslands, in most places shrub species are dominant and are important in livestock diet. In some areas shrubs and cacti compose the whole diet, because grasses and other herbaceous vegetation are lacking.

We have not yet identified the most satisfactory utilization practices for every shrub or cactus species in northern Mexico, to obtain a maximum sustained production. The data presented in this paper are based on the experience of many range managers and direct observations by the author and coworkers in Rancho Experimental La Campana, INIP-SAG. and in other Government agencies during several years. The aim has been to determine the traditional practices of utilizing shrub-grass plant communities in northern Mexico and to evaluate many shrub and cactus species as forage.

In arid zones we should not expect to have a solid cover of grasses; we do not want to exterminate several excellent woody or succulent species. On the contrary, there is evidence that some valuable forage shrubs are desirable in open grasslands, especially during the dry winter and spring months, and even more during the frequent drought periods, lasting several years, that are common in northern Mexico.

Traditional management practices on rangelands in northern Mexico are characterized--with some exceptions--by overgrazing; this is why several million hectares of once highly productive grasslands are at the present time deteriorated (CFAN-CID 1965), producing near their lowest limit, and invaded by undesirable species. Often a young range surveyor has a hard time deciding whether to classify a given area as a grassland invaded by woody species and in poor or fair condition, or as a shrubby type in good condition.

In our territory in northern Mexico, we lack long-term information about the pristine or climax status of several areas, making it difficult to determine with accuracy their successional stage. This is particularly true of the shrub-grass plant communities. Studies have been underway since 1964 on the inventory of range resources of northern Mexico (CFAN-CID 1965; COTECOCA-SAG. 1969), and these have made possible the determination of the major vegetative types, the different range sites within each type, and the forage production, availability, and utilization of each site. These studies were sponsored by the cattlemen's associations of eight States and by the Federal Government. This has been the first serious technical approach in obtaining the basic data to structure the new reforms of land tenure systems in Mexico.

Six important shrub-grass communities in northern Mexico

In the natural pasture lands in northern Mexico, six vegetative types illustrate the importance of shrub species in the livestock economy of this area and some of their management implications. Very accurate utilization figures are still not available for all the communities; however, it has been possible to make some acceptable estimates. The accounts which follow describe only those plant species for each type which determine the physiognomy of the community, and those which are important in the diet of domestic animals.

Larrea-flourensia

Characteristic of the Chihuahuan desert, this community is found in over 10 million hectares (24,710,000 acres) in northern Mexico, in areas where annual rainfall varies from 180 to 250 mm. (8 to 10 in.). It is found mainly in the States of Chihuahua, Durango, and Coahuila. Soils where this community prospers are generally light colored, calcareous, ranging from sandy loam to clay loam; topography is flat or slightly rolling.

Vegetation is dominated by *Larrea tridentata* and *Flourensia cernua*. Other woody species present are *Acacia constricta*, *A. greggi*, *Parthenium incanum*, *Fouquieria splendens* and, in the lower, deep-soil sites, *Prosopis juliflora*. Perennial grasses are scarce, and are only present in the lower areas, where there is additional water runoff from adjacent slopes. They never form continuous, solid stands. These perennials are mainly *Hilaria mutica*, *Muhlenbergia repens*, and *Scleropogon brevifolius*. Growing protected by shrubs, *Muhlenbergia porteri* is another important component of the community.

Forage for livestock is provided mostly by annual grasses like *Aristida adscencionis*, *Chloris virgata*, and *Bouteloua barbata*, which are readily utilized by livestock during the short rainy season (July to September). Perennial grasses, even when dry, are almost the only source of forage during the rest of the year (fig. 1A). Production in normal years is expected to be around 60 to 80 kg. (132 to 176 lb.) of usable forage per hectare.

Bordering vegetative types may be halophyte grasslands on the lower slopes with *Hilaria* and/or *Sporobolus*, and *Agave-Yucca* communities in the adjacent rocky hills.

According to data collected in the inventory of range resources in northern Mexico (CFAN-CID 1965), 86 percent of the land where *Larrea-Flourensia* communities are dominant sustain a yearlong cow-calf operation, and the remaining 14 percent are seasonally utilized by steers or heifers. Although management makes the basic difference in productivity between vegetative types, calf crops in the *Larrea-Flourensia* areas were found to be less than 60 percent in 52 percent of the sampled ranches; weaning weight of calves averaged less than 150 kg. (331 lb.) in 71 percent of the ranches.

Of the methods used to improve forage production in this community, water and soil conservation are the most important. Seeding has proved successful when water catchment

structures are built. Los Pozos ranch, for example, near Aldama, Chihuahua, increased forage production over 500 percent by seeding *Panicum antidotale* (blue panic grass) and *Sorghum almum* in an area with 250 mm. (10 in.) rainfall per year. Numerous native and introduced grasses are being tested.

Atriplex-Prosopis-Sporobolus

Most of this vegetative type is found in the northern part of the State of Chihuahua, in the Vizcaino region in Baja California, and in the Laguna region around Torreón. Annual rainfall is less than 200 mm. (8 in.) (some areas 60 mm. (2 in.)) and the soils are sandy, forming dunes in most areas.

Dominant shrub species are *Atriplex canescens* and *Prosopis juliflora*, which serve as soil stabilizers. During the short summer rainy season, numerous ephemerals appear, some of which are consumed by livestock. Perennial grasses, although never forming solid stands, provide good forage during the whole year; these are *Sporobolus flexuosus* and *Panicum havardii* in the most sandy sites, and *Sporobolus airoides* in the lower areas where soil is heavier.

Atriplex canescens and, to a lesser extent, *A. nuttallii*, are among the most important forage plants in the community, particularly during the dry months (November to June); these two species have high protein levels even in the winter, and supplemental feeding of livestock is almost unnecessary where they are abundant. *Prosopis juliflora* is browsed when new leaves and twigs appear in the spring and nothing else is green (fig. 1B).

Production of usable forage is around 110 to 170 kg. (243 to 375 lb.) per hectare per year (COTECOCA-SAG. 1969). Information supplied by the inventory of range resources (CFAN-CID 1965) indicates that 76 percent of the *Atriplex-Prosopis-Sporobolus* communities in northern Chihuahua are grazed yearlong in cow-calf operations, and the rest is used only during the rainy season. Information on livestock production in this area is limited; however, three large ranches in northern Chihuahua report long-term average calf crops from 62 to 75 percent, and fall weaning weights of 148 kg. (326 lb.).

Improvement practices in this plant community would necessarily include sand dune stabilization with forage grasses or shrubs. Trials are under way on establishment of such species, including some of the genera *Haloxylon, Calligonum, Kochia,* and *Atriplex.* More information is also needed on revegetation of these sandy areas and on the behavior of domestic animals under different grazing systems, particularly in the Vizcaino region of Baja California.

Agave-Yucca-Bouteloua

This community covers numerous scattered rocky hills and sierras throughout northern Mexico, mainly in the States of Chihuahua, Coahuila, Durango, Nuevo León, and San Luis Potosí. The hills are generally surrounded by the microphyllous desert, where rainfall seldom reaches 300 mm. (12 in.) annually. Soils are rocky and calcareous; topography is very steep, and some places are inaccessible for animals.

Vegetation is dominated by rosette-type, fibrous plants, such as species of *Agave, Yucca,* and *Dasylirion. A. lecheguilla* is characteristic in almost the total area. Other shrubs include *Fouquieria splendens, Calliandra eriophylla* and *Euphorbia antisifilitica*; from these, only *C. eriophylla* is browsed by animals, and sometimes the *Yucca* flowers, when ranchers cut them off and the animals eat them on the ground. The forage species are *Bouteloua breviseta*, as the most abundant, *B. gracilis, B. curtipendula, Aristida pansa* and, in minor amounts, *Tridens muticus* and *Heteropogon contortus.* All of these are available year round, but *B. breviseta, H. contortus*, and *A. pansa* are utilized mostly during late spring, summer, and early fall. Annual grasses are not very abundant, but they form a part of the animal diet during the rainy months (fig. 1C).

Figures on livestock production have not been obtained because animals do not live in this area all year long. It is very rare for an entire pasture to include only this plant community; the topography is rough and sometimes the *A. lecheguilla* is so dense that animals cannot walk through. Also, water for livestock is difficult to obtain in these hills. Forage production has been determined to be from 175 to 250 kg. (386 to 551 lb.) per hectare in normal years.

Perhaps the only improvement practice recommended for this plant community would be a selective hand clearing of *A. lecheguilla* and other inedible shrubs and succulents, to leave more space for grasses.

Opuntia-Acacia-Bouteloua

A very interesting and productive community, this vegetative type covers a considerable area in the States of Durango, Zacatecas, and San Luis Potosí, where annual rainfall may average up to 500 mm. (20 in.). It is found exclusively on volcanic, somewhat rocky, reddish soils, both in plains and in low hills.

The most characteristic species is *Opuntia leucotricha*, a long-stemmed cactus that maintains a good population of perennial grasses under its canopy. *Acacia farnesiana* is a second dominant shrub. Other woody plants in the community are *A. greggi*, *Condalia mexicana*, and a little *Prosopis juliflora*. The excellent grass cover under *Opuntia* is composed mainly of *Bouteloua gracilis*; other grasses present are *B. curtipendula* and *Hilaria belangeri*. These grasses are the main components of the livestock diet; however, other very important components are the fruits of *O. leucotricha*, particularly during late summer and early fall. Cattle eat even the succulent cactus stems during the dry months, November to May (fig. 1D).

Ranchers affirm that *Opuntia-Bouteloua* communities yield more beef per hectare than the open grassland, and that the need for winter supplements is much less. In some places, however, *Opuntia* stands are so dense that cattle cannot walk through; opening lanes may result in a recovery of perennial grasses.

One of the problems in this community is the heavy population of *Acacia farnesiana*, an undesirable shrub or tree that provides no forage.

Data provided by the inventory of range resources (CFAN-CID 1965) indicate that the *Opuntia-Acacia-Bouteloua* community is used only under cow-calf operations yearlong, and that 77 percent of the sampled ranches have a calf crop between 61 and 80 percent; the remaining 23 percent falls between 41 and 60 percent. Weaning weight of calves in this vegetative type averaged 163 kg. (359 lb.).

Livestock production in these areas may be improved considerably by brush control (*Acacia* and *Prosopis*); experiments in Durango showed this to be possible. It is not recommended to exterminate *Opuntia leucotricha* until more information is available; so far, it is recognized as a valuable forage for cattle. Clearing of land and seeding have good possibilities. Fertilization with nitrogen and phosphorus in Durango has demonstrated also that production can be significantly improved with this practice.

Acacia-Leucophyllum

This community is almost exclusive of the northeast part of the State of Coahuila, where annual rainfall is from 350 to 400 mm. (13 to 16 in.). Soils are calcareous, and are shallow in foothills and ridges and a little deeper in depressions.

The physiognomy of this vegetative type is one of "chaparral," where medium-height woody species are dominant. There is abundant cover of grasses that combine with shrubs

for an excellent livestock diet. *Acacia berlandieri* and *Leucophyllum texana* are the most abundant shrubs. *A. berlandieri* provides an excellent and abundant forage for cattle and goats. *Porlieria angustifolia* is also good, although not as abundant. *Prosopis juliflora* occurs mainly in the lower sites and is browsed by cattle and goats in the early spring, but is never an important diet constituent (fig. 1E). Several good perennial grasses are associated with the shrubs; *Bouteloua gracilis*, *B. curtipendula*, and *Hilaria belangeri* are the most important. In deeper soils, where more moisture is available, *Panicum obtusum*, *Hilaria mutica* and *Sporobolus airoides* may be present. Most of the yearlong forage is supplied by perennial grasses, but undoubtedly *A. berlandieri*, *L. Texana*, and *P. angustifolia* make a very important contribution to the overall forage and livestock production of this area. Perennial grasses produce from 450 to 600 kg. (992 to 1,323 lb.) per hectare of usable forage.

Ninety-two percent of the ranches within the *Acacia-Leucophyllum* region are dedicated to a cow-calf operation, according to the inventory of range resources (CFAN-CID 1965). This same inventory reports calf crops of 70 to 80 percent in 87 percent of the ranches. Weaning weights are between 161 and 175 kg. (295 and 363 lb.) in 54 percent of the ranches, and above 176 kg. (388 lb.) and up to 220 kg. (485 lb.) in 39 percent of the ranches.

Improving livestock management practices alone could result in higher yields of beef per hectare, as demonstrated by some ranches in the Zaragoza area, where calf crop is around 90 percent and weaning weights of calves in the fall reach over 220 kg. (485 lb.). Undesirable brush, like *Prosopis*, is being controlled extensively in the area. In lower sites, buffel grass (*Pennisetum ciliare*) has been planted with excellent results.

Cercidium - Olneya - Bouteloua - Cathestecum

This plant community, a component of the Sonoran desert, is found in the north-central part of the State of Sonora, where annual rainfall averages 280 mm. (11 in.), in flat plains with deep, sandy to sandy loam soils. Although most of the rain falls during the summer, sometimes winter rains may occur in December and January ("equipatas"), yielding a good crop of ephemerals in the spring.

Among the numerous woody species abundant in this type, *Cercidium microphyllum*, *C. sonorae*, and *Olneya tesota* are the most characteristic. Other important components are species of *Bursera*, *Prosopis*, *Larrea*, *Acacia*, *Encelia*, and succulents like *Lemaerocereus*, *Pachycereus* and *Opuntia*. The grass population is dominated by *Bouteloua rothrockii* and *Cathestecum erectum*, which constitute most of the usable forage for livestock; these green up during the summer with the rains, but even in the rest of the year, when dry, they are readily eaten by animals. Livestock eat the flowers and tender pods of *Cercidium* and *Prosopis* in the spring, mostly from April to May, and also browse the young leaves of *Olneya*. Cattle eat the flowers and fruits of *Lemaerocereus* when they fall from the tree to the ground (fig. 1F).

Most of the ranches in this region of Sonora support a cow-calf operation (76 percent); however, a few others have a combined operation, buying and selling steers and heifers to use the range only during the rainy season (CFAN-CID 1965). Forty-eight percent of the ranches have calf crops from 41 to 60 percent, and 44 percent of the ranches have from 61 to 80 percent calf crops, according to information provided by the inventory of range resources (CFAN-CID 1965). Only 25 percent of the ranches produce calves of over 151 kg. (333 lb.) weaning weight, an indication of the potential for improvement of livestock production.

Range improvement practices presently used include clearing of brush and seeding with buffel grass. Range pitting and subsoil plowing have been used also with good results.

Conclusions

This paper has described some of our shrub-grass plant communities in northern Mexico, giving more emphasis to management problems than to taxonomic or ecological features. Controversy has arisen here, as in other areas, over the value and the problems represented by shrubs and cacti. I believe we must learn to live with these plants in arid lands and make the best possible use of them.

A great deal more information is needed on the value of shrubs and cacti in producing and sustaining millions of livestock in our desert environments. Research in this field is now, and will be in the immediate future, directed toward the following aims:

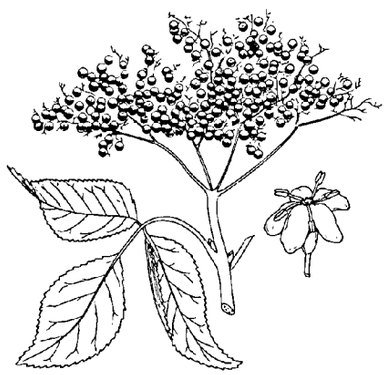
1. To determine forage production of shrubs and cacti, and the availability of this forage through the year.

2. To determine the preference and utilization by livestock of shrubs and cacti.

3. To determine the nutrient content of these plants, and their seasonal and yearly fluctuations.

4. To determine the most efficient propagation and establishment methods of selected shrubs and cacti in desertic zones.

All who have lived in and dealt with the resources of arid zones and have observed how domestic animals sometimes thrive in apparently unfavorable environments will agree that their ability to do so is due, in great part, to the shrubs and cacti that give the desert its characteristic landscape.



Integration of shrub research effort

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Research is either static or dynamic--concerned with what is or what happens, states, or processes. In either case, the purpose may be descriptive or interpretative. Static descriptive research on shrubs and shrub ecosystems would include taxonomy, pedology, and vegetation analysis. An example of dynamic descriptive research would be a project concerned with measuring the foliage consumption of different herbivorous insects.

Interpretative research, even when directed to interpretation of a static situation, can hardly remain static. Such a project might, for instance, be an examination of differing vegetation pattern as a function of grazing pressure. This project, though concerned with the pattern *as it exists*, would inevitably involve the processes of herbivory and crop regrowth; thus, it would require a dynamic approach in order to interpret a static situation. Of course, most dynamic research also has an interpretative goal; such would be, for instance, a project to study the effect of shrub chaining on meat production from rangelands.

The objectives of research usually go beyond either description or interpretations; they are predictive. In the most modest form of prediction, one merely wishes to be able to extrapolate static or dynamic observations to situations at present unobserved. But often prediction in the strict sense is called for--extrapolation from the present to the future.

Prediction is always involved in applied research. The application lies in the future and only in virtue of the predictive power of research conducted today can it be applied tomorrow.

Even when research has no application in view, predictive power is important. If the description and interpretation are correct, they will enable the investigator to make correct predictions and the correctness of his predictions will be the test of his interpretations.

In any research program, the first step should be to set one's objectives--the questions one wishes to answer. And they should be specific as clearly and precisely as one can, otherwise their attainment will be equally unclear. You will note that I use the plural; this is deliberate. There are considerable advantages in combining several objectives in a single research program.

However, at this point, let us consider research directed toward a single goal; for example, determining the effects of fertilizer on quality of forage from shadscale, *Atriplex confertifolia* . Let us set as our precise objective an answer to the question: "What is the effect of different levels of superphosphate application up to 500 kg./ha. in spring on the protein content of *Atriplex* foliage during the three subsequent growing seasons?"

In any research, one must be concerned with the range of relevance of the results. If they relate only to the specific subject matter of the observations--the particular individuals or the particular area, the actual time interval, and the specific set of environmental conditions in which an experiment was performed--the work is almost nugatory. Inasmuch as the same time interval cannot recur, the individuals might be dead, and the set of environmental conditions can never be duplicated exactly, the results can never be applied to any real-life situation. Clearly, one needs to be able to say that the particular subject matter of the research was in some defined sense representative of a whole population or universe of similar subject matter.

In our shadscale nutrition problem, one might have set up a replicated field trial to answer the question. And one might have obtained answers having a high degree of precision for the particular conditions of that trial. But if the trial had been located elsewhere, would the same answers have applied? If it were conducted in another season, would the same answers hold? One could improve the situation by continuing the trial for several seasons, or by replicating it throughout the Great Basin. Then, at least, one could express the answers in terms of a mean expectation. Or, of one had made some concomitant measurements--soil analyses, or meteorological records--one might be able to express the variation in results as an empirical function of these influencing factors.

The extrapolation of the results of research to a universe of reference is usually performed after the event by intuition or guesswork. This is clearly unsatisfactory. It is far better to define beforehand the universe to which one's results should be applicable, and design the research so that the interpolation or extrapolation needed will be valid--or at least plausible. If this universe is enumerable, or extends continuously over certain dimensions (the earth's surface, for instance) randomization with or without stratification may be needed. Randomization without stratification is generally appropriate only if some sort of central estimate is required, or if the universe is thought to be uniform. Generally, one recognizes that the results will vary over the universe, and one needs information about this variation. If variation in the universe can be expressed in terms of certain factors that may influence the results observed, this influence can be incorporated into the results by regression analysis; a wide coverage of values of these factors is then required, rather than a random distribution through a universe that may well have ill-defined limits. Alternatively, a classification or categorization of the universe may be appropriate; if so, the samples should be stratified.

In our example, it is obvious that we would aim at wide geographic coverage, seeking results that could be applied to most or all soil types and meteorological patterns that we might encounter within the geographic range covered. But we would also wish to include the different vegetation types in which shadscale occurs, different types of grazing pressure, and perhaps varying seasonal patterns of insect and herbivore damage. The number of variables in the universe is large; when one considers that timing of events may be all-important in determining their results, their numbers become infinite. One quails before the thought of covering a useful selection of such variables in factorial experiments, or even by a regression analysis of the results of replicated experiments in which they might vary in an uncontrolled fashion.

Taxonomy is almost the only research field where attempts have consistently been made to cover the whole universe of reference. In this field, it is customary to bring together as wide a range of specimens as possible before revising the classification of a group. In other fields of research--including the whole of shrub research--it is highly exceptional for steps to be taken to ensure that the whole of the relevant subject matter is covered, even when the investigator has a clear picture of what this universe includes.

Shrub research rarely deals with the shrubs in isolation. Generally, this is true of descriptive projects in taxonomy and of some in anatomy, cytology, and similar

fields. When we are concerned with dynamic processes in the shrubs within their natural environments--specifically, with relations between shrubs and other plants or animals, the results will be dependent on the conditions in the rest of the system. "System" is the keyword. The shrub is part of a very complex system, penetrated throughout by numerous interlinked causal chains; if any part of it is isolated in thought, there are grave risks that conclusions drawn will be false because important interactions have been ignored.

Let us consider the question we have posed of changes in the protein content of shadscale foliage as a result of superphosphate application. The fertilizer first has to enter the soil--a process that will depend on rainfall and infiltration, as well as, perhaps, on activity of soil animals. In the soil, the fertilizer may be immobilized by physiochemical processes or by micro-organisms, and may then become available at some later time to be taken up by roots of the various species present. The uptake by any particular species will depend on (1) competition from other species, (2) the physiological state of the plant, and (3) the moisture content and availability of other nutrients in the soil. The phosphate added may also affect the uptake of other nutrients.

The changed ratios of nutrients taken up from the soil will modify the behavior of the different meristematic regions of the plant; however, their actual activity will also depend on a host of other factors, including the existing proportions of different organs, their physiological state, and the amounts of labile carbohydrate available. The amount of active meristematic tissue will also depend on present and recent meteorological events, and on recent patterns of herbivory. The latter in turn will depend on the populations of herbivores of different species, including insects, and on factors affecting their behavior, such as the availability of alternative food plants. Herbivore populations will depend on previous primary productivity and carnivore pressure, among other factors. All these factors, in addition to the nutrients taken up from the soil, will thus affect the proportion of shrub organs, their age distribution and their chemical composition and, hence, the protein content of their foliage. Thus one can trace causal chains or networks that will be influenced to a greater or lesser extent by every element within the ecosystem. Consequently, the effect of fertilizer on the protein content will be influenced by every component of the ecosystem, and by every factor impinging upon it. The results of a direct field experiment on such a system can only hold for the particular sequence of values for the other variables that were obtained during the course of the experiment. If one wishes the results to be of more general applicability, one needs to know how changes in these influencing variables will affect the results--including the quantities of other species, plant and animal, within the system--or, one needs at least good grounds for deciding that some of them can safely be ignored.

The fact that the questions posed are usually within the ecosystem context, and that a sound solution requires study of a wide range of components and processes additional to those explicitly included in the objectives suggest that research strategy should concern itself very seriously with the *completeness* of studies of the ecosystem. It is wise to start by making a reasonably complete map of the ecosystem. One can then see which of those processes peripheral to the main subject are already well enough known to indicate the extent and direction of their effects, which of them can be ignored with minimal risk, and which on the other hand are potentially important enough to warrant special study. If the range of investigation needed is too broad to be practicable, a preliminary survey may suggest that a study of the effects in question is hardly worthwhile. Alternatively, it may suggest how the universe to be covered can be restricted to make the work less ambitious but practicable. On the other hand, it may show that one or two supplementary studies would be sufficient to increase the scope of the conclusions reached.

Since such a general mapping of the ecosystem would be required for any research project on the behavior of shrubs or other components within the ecosystem context, there are clear advantages in arranging for a number of research projects concerned with the same ecosystem to join forces for this operation. Many of the processes in the ecosystem will affect the results of several (perhaps all) of these projects; if they need special study, this should clearly be done collectively, rather than separately and repetitively.

A general survey of the ecosystem processes that may influence the effect of the one that is being examined is valuable. Such a survey's value will be enhanced if it is cast in the form of a computer model.

Computer simulation of ecosystems first saw the light of day some 10 years ago. It is based on the assumption that the composition and structure of the ecosystem at any moment of time can be expressed by the numerical values of a set of variables including, for instance, the biomass and composition of different species, the soil moisture in different parts of the area, and populations of different animal species. It is further assumed that the changes in each of the endogenous variables with time can be expressed as mathematical equations in terms of these and other measurable quantities such as meteorological variables ("exogenous variables"). If the value of the endogenous variables are known at a particular time, and the values of exogenous variables are specified for a period thereafter, the equations can be solved and the values of the endogenous variables at the end of the period calculated. Using successive calculations like this, the behavior of the whole ecosystem over a long period can be simulated, and any modification proposed can be introduced, and its effects consequently can be predicted.

A useful computer model of an ecosystem is usually based on a rather detailed analysis of its structure and functioning. Each of the equations involved is an expression of the current level of understanding as to how the rate of change of some component is influenced by other factors, some of which may be internal to the system, others exogenous. Thus, the rate at which phosphorus enters the root system may be a function of the root concentration in different horizons, the concentration of available phosphate and other ions, the water content and the temperature in each of these horizons, together with the current rate of transpiration. Though all of these may be endogenous variables, the transpiration rate, for instance, will in turn be dependent on the exogenous variables of atmospheric humidity, temperature and wind, while the temperature profile in the soil will depend on radiation. As a whole, the model will consist of a large number of expressions like this reflecting the mechanisms of a particular portion of the ecosystem.

Rather than perform an empirical experiment to answer the question as propounded, one might break the problem down into a number of simpler components and tackle each of them separately in order to provide reliable building blocks for the computer model. It would not be easy to devise and carry out experiments to determine the function connecting phosphorus uptake with the aforementioned factors. However, to answer the questions in temporary isolation from the rest of the ecosystem would be far easier than to answer them from empirical experiments on the whole ecosystem where (a) the soil-profile factors were only a few of the whole suite of variables affecting ecosystem functioning; (b) one was not observing the rate of phosphorus uptake directly but deducing it from changes in the phosphorus content of the foliage; and (c) the effects were being integrated over a substantial observation period during which many of the relevant conditions were changing.

Computer modeling is a powerful tool for the ecologist and resource manager to use in interpreting ecosystem behavior. Assumptions about the ways in which different parts of the system interact can be incorporated in the model; then, the performance of the model can be compared with real-life ecosystems. Extrapolation to unobserved sets of conditions can then be based on an understanding of the mechanisms involved.

A suitable integrated approach to research on the functioning of wildland shrubs would involve the following steps:

1. Define a set of objectives, in terms of questions to be answered. These questions will commonly take the form of asking the effect on some part of the ecosystem of a modification imposed somewhere else. There may be economical advantages in asking several questions at the same time.

2. Define the universe to which the answers are to apply including the geographical range, differences in biotic composition, and ranges of values for each variable in the system.

3. Design a model of the ecosystem that will provide answers to the questions posed, making use of the best available information regarding the forms of functions and values of parameters involved. Code the model as a computer program.

4. Take one by one the state variables not directly required as answers to the questions posed, and run the computer model twice for each variable, with its initial value set respectively at the maximum and minimum of the range specified in step 2, while the other variables are initially at their midpoints. Those variables for which the two runs differ only negligibly can then be held constant at their midpoints, and the functions expressing their rates of change can be dropped from the model. (Strictly, these tests should be conducted factorially, with maximum and minimum for the different variables being combined in all possible ways. In most cases, however, the number of combinations would make such an approach impracticable).

5. Divide the model into portions convenient for experiments that will enable its accuracy to be tested within the whole range of input values expected and also provide for improved estimation of parameters where required. Perform the experiments indicated.

6. Recode each submodel on the basis of the experimental results, and combine the submodels into a complete ecosystem model.

7. Establish a number of field trials in a variety of situations covering as large a part as possible of the relevant universe. These field trials should include measurements of all the inputs required by the model, together with the outputs constituting answers to the questions posed.

8. Operate the ecosystem model with the inputs derived from the field trials, and compare the outputs with those observed. A bias indicates a fault in the model; variation between observed and expected results affords an estimate of the error of prediction.

An ecosystem model answers the questions posed as objectives in a much more satisfactory way than would a field experiment of the usual type. It offers answers that are recognized as depending on, and varying with, all the factors influencing the relationship in question. The answer is many-dimensioned; the usual field trial constitutes a few-dimensional (often one-dimensional or even no-dimensional) section of it, and even within this section may not cover the whole universe of interest.

Some approaches to achieving the potential of shrubs for man's use

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The question confronting us is "How do we reach the potential that has been expressed for shrubs?" In order to do this, I think we must examine the problem thusly: First, what is the setting in which we must achieve the potential of shrubs? Second, what is that potential? And third, how do we set up an organization, structure, or mechanism by which we can reach the potential that has been expressed?

The setting in which the potential must be achieved

If we lump together all of the land on which shrubs are the major vegetative resource, we find that well over half of the exposed land surface of the earth is covered in some form of low-grazing woody vegetation. These forms include scrub forests, grazing lands of savanna areas, and desert regions. The major use for most shrubland ecosystems is for grazing by wild or domestic animals.

Productivity cannot be maintained on these lands if they are managed using standard agronomic practices. Intensive management is seldom profitable or possible. The science of ecology forms the basis for decisions on land use where shrubs normally occur and where management is usually of an extensive (low input) nature.

Although low-growing woody vegetation might occur in any climatic area, by far the major portion of shrubland ecosystems occurs in the arid regions of the world. Furthermore, many of these lands are in the developing countries where economic and social institutions are not as advanced as in many of the more humid regions.

Therefore, there are some rather severe restrictions and constraints on achieving the potential of shrublands. These should be examined in detail before structures for achieving shrub potential can be developed.

Climatic environment

Not the least of these constraints is that imposed by climate. The average shrubland ecosystem is characterized by low and undependable rainfall (McGinnies and others 1968). This precipitation is poorly distributed spacially, seasonally, and yearly; this causes uneven, and often unpredictable, levels of biological productivity. Prolonged droughts are common and to be expected (Heathcote 1969). Total amounts of dry matter produced can vary 300 percent or more between years within a climatic cycle.

Storms might produce adequate rainfall for plant growth on a given portion of a shrubland ecosystem while on another area, only kilometers away, no rainfall occurs. This pattern contributes to rather ineffective use of moisture produced by rainfall and contributes to the concentration of animals or plants in areas that have received rainfall.

Seasonal moisture distribution usually limits growth to one period of the year and determines the types of shrubs that inhabit an area. Extreme examples vary from cold desert shrublands where plant growth is related to the amount of moisture from

snowmelt in the early spring to tropical scrub areas where growth is initiated monsoonal storms occurring only a few months during the year.

Biological constraints

The severe climatic restrictions impose equally severe biological constraints. Productivity of dry matter is usually low and highly variable. Plants have evolved for survival rather than high productivity. The modifications that have developed to allow plants to survive the rigorous climatic conditions imposed in arid lands are not usually associated with great production of biomass. Such modifications as dormancy, curling, or dropping of leaves, etc., might enable plants to withstand the severe condiions of deserts, but these same plants might not produce forage or usable products for man. In addition, many of the modifications for survival make plant material deter efficient grazing by domestic animals.

Cattle and sheep, in particular, find that the modified leaves, stems, and thorns are a major deterrent in feeding. Goats and camels can make somewhat better use of the shrubs of dry areas but even they might not be as efficient in their use of some shrubs as the native animals that feed upon the plants. Recent unpublished work in East Africa (M. Gwynne, personal communication) shows that the shrub diet of many of the wild ungulates is directly related to the morphology of the mouth parts of the animals.

The plants of arid regions have seldom developed under continuous grazing. Instead, they have evolved under a system of shifting and nomadic use geared to the spotty rainfall patterns. Attempts to change the pattern of use and to obtain greater yield of animal products many times lead to a deterioration of plant community and a loss in the composition of the more stable plants (Box 1971).

Shrubs usually evolved under browsing by a variety of herbivores ranging from invertebrates to large browsing mammals. Attempts to change this pattern of use and impose heavy continuous grazing by one class of domestic animals might lead to a loss of the more desirable shrubs from an ecosystem.

Shrubland ecosystems are delicately balanced and, for the most part, succession is extremely slow; therefore, once an ecosystem has been disturbed or altered, it seldom heals itself within the lifetime of a man. Artificial restoration of damaged shrubland ecosystems is also difficult because of the rigorous climatic and biological constraints imposed upon such systems.

Social restrictions

The climatic and biological restrictions may be recognized by people charged with the settlement and development of arid lands, but the ecological implications of these restrictions seldom are related to the lives of the people who inhabit the deserts of the world. Equally as important as the physical environment, but usually not as well understood, are the sociological and economic restrictions that are imposed in the arid shrubland regions of the world. For instance, most arid shrubland areas have a low human population density. As a result, the lack of support for public funding of projects (development or research) in range areas of large countries having uneven population distribution is not related to need so much as to the perception of priorities by the people living in the high population areas (Perry 1969) where the political powers also are concentrated. When a small country is located entirely within an arid area, it might lack the ability to support its own development; such countries have learned that the world community does not view its development projects as high priority items.

Support facilities and services are poor or lacking in many arid regions. Communication between individuals and groups of people is usually difficult. Transport facilities are poor or lacking entirely; in many areas, this restricts the ability to move produce to market (Hartley and others 1966).

The isolation of people in the arid areas has tended to make them self-sufficient. They are strongly individualistic and usually tend to act on their own initiative rather than collectively. The traditional land use of much of the arid shrubland areas is a nomadic pastoralism. The nomadic habit is generally discouraged in developing countries, but the "nomadic sector" has been identified as a major force in economic development in some arid shrubland regions (Konczacki 1967). The traditional movement of people and livestock throughout the shrublands usually fits the physiology of the plants and the general ecology of the plant community (Box 1971). Therefore, although not popular with politicians in many countries, nomadism may be the best form of land use of arid shrublands.

Social institutions serving the shrubland areas of the world are usually weak. The combination of a low population with little political organization usually tends to have the arid regions underrepresented in organizations and structures affecting decisionmaking about development and/or land use.

Research efforts to obtain data necessary for development are scattered and poorly funded. The tendency in most countries has been to finance research efforts that relate most directly to the largest number of people. Hence, research programs in the nonarid areas have had the highest priorities.

Economic restrictions

Sociological factors are further complicated by rather severe economic restrictions. The arid regions offer a high risk with low returns to investment. There are almost no financial institutions geared specifically to the development of the arid regions. The use of arid regions requires a unique financial structure if full development is to be achieved. Loans must be long term in nature in order to cover two or more climatic cycles. Repayment schedules should be geared to the "feast and famine" conditions of production characteristics of shrublands. Until venture capital is available under conditions specifically designed for arid areas, little sound development can take place in arid shrublands.

In summary, the setting under which we must try to achieve the potential of shrublands is harsh. Precipitation is low, biological productivity is erratic, and practically no social or economic institutions have developed to aid economic development. The value of shrubs and shrublands is potentially high, but reaching the potential will be difficult.

Biological potential of shrubs

Potential for forage

The most important single use of shrubs is as food or fodder for grazing animals. Although some products from shrubs will be used by human beings directly, most of the products valuable to human beings will come through animal products. To date, most of the emphasis in using shrubs has been on traditional domestic livestock breeds. Sheep and cattle have attracted by far the most attention, but these may not be the most efficient animals in arid areas. Other traditional livestock, such as camels, goats, and donkeys, have been shown to be much more efficient under harsh, dry conditions (MacFarlane 1968). Even within the traditional sheep and cattle species, little has been done with traditional, local varieties especially adapted to utilizing shrubs in the arid and shrubby regions of the world. Many of the sheep breeds of the Middle East, East Africa, and the Asian subcontinent may be much more efficient in utilizing the shrub regions than the British and European breeds that have been imported into these areas. By the same token, slow growing but efficient cattle, such as the Boran of East Africa, may be more important in utilizing shrubs than some of the rapid growing "bred-for-feedlot-conditions animals produced in the United States.

Many wild ungulates offer a new and unexploited avenue for converting shrubs to animal products: the eland and oryx of East Africa; the ibex of the southwestern Asian mountains; and the wild sheep and goats of the Indian subcontinent stand. These animals could be used for sport hunting, for game cropping, or could be domesticated and managed.

The utilization of arid shrublands for high production of animal products is a complex problem involving biology, sociology, and economics. The most efficient biological solution may not be acceptable to people who buy the products from the men on the land. For instance, let us assume that greater biological efficiency in shrublands could be obtained by removing cattle and sheep from the environment and stocking the same ranges with donkeys, goats, and jackrabbits. Even though larger amounts of good, nourishing, red meat might be produced, acceptance of the products would not be sufficiently high to allow the change to be profitable. Much more must be done on social and economic factors relating to shrub use before the potential can be achieved (Box 1969).

More work must be done on systems of management for shrubs if their full value for livestock forage is to be realized (McKell and others 1969). Harvest methods should also be improved. Lopping of tall shrubs and trees for forage is practical in Australia (Everest 1969) and on the Indian subcontinent (Kaul and Gangali 1963) during drought periods. Preserving shrub and cacti parts as hay or silage might offer increased production (Martinez 1969).

Building products

Little has been said in this Symposium about the value of shrubs for building products. The frames of houses and huts in the arid regions of the world, the mine timbers for shafts that go under hillsides of arid regions, and the air-conditioner cores that form the evaporative cooling in many desert regions of the world all come from the woody parts of shrubs. Potentially, this large resource of woody plants offers tons of cellulose that could be used to manufacture particle-board, molded furniture frames, and many specialty items. Special attention should be given to using cellulose of plants cut or uprooted in type conversion projects.

Fuel

Likewise, in a conference held in a developed country, the value of shrubs for fuel is sometimes overlooked. The cooking and warming fires of many people in the more remote and arid regions still come from shrubs. Charcoal is a valuable commodity in many areas. Recent kilns developed in Kenya indicate that small twigs and branches from shrubs can be converted to charcoal with little waste and that the charcoal produced can be a valuable by-product of range improvement schemes (Little 1971).

Food

The potential of shrubs for enhancing the health and leisure time of the human animal should not be overlooked. Many shrubs produce valuable fruits and nuts that once were the livelihood of aboriginal man. Today they form the basis of jellies and party favors that greatly enhance the quality of life, and there are indications that the cellulose from the woody stems of shrubs can form the basic medium for growing protein-rich organisms that could feed man.

Landscaping

The shape, form, and color of shrubs add to the natural beauty of the desert scene that has long enhanced man's enjoyment of a rather austere environment. These same shrubs can be used to beautify cities, suburbs, roadsides, and other restricted environments where water is scarce.

Religions and pleasure uses

Products from shrubs have long been used for producing various esthetic or religious experiences. Frankincense and myrrh have been used in religious ceremonies for many centuries. Other chemical extracts from shrubs have been used for stimulants, hallucinogens, and mind expanding experiences long before the youth culture of the western world discovered them. The discovery of them by today's youth and the apparent acceptance of the current generation of many types of pleasure drugs opens a whole new field for shrub use. Before this field can be exploited, much legal, social, and psychological research needs to be done.

Organizing to reach the potential

The potential for shrub use for the good of man is great. But the environment where shrubs grow best is harsh, and the social, political, and economic institutions that are needed for the development of shrublands are weak.

During this Conference, an *ad hoc* committee met and recommended the establishment of an International Advisory Committee to identify needs for action and research programs. They suggested the following:

1. Improve communication between scientists by publishing a proceedings and establishing a newsletter.

2. Develop an inventory of shrub research and knowledge. Encourage an international agency to publish the material and keep it current.

3. Organize a committee to coordinate research efforts on a worldwide basis.

4. Identify research areas necessary for increasing production in shrubs. Establish priorities for action programs.

5. Establish a program for exchange of knowledge, scientists, seeds, and equipment.

6. Plan a future meeting in 3 to 5 years to examine progress since this Congress.

If these specific objectives can be met, the potential for increasing shrub productivity is great.

Section IX.

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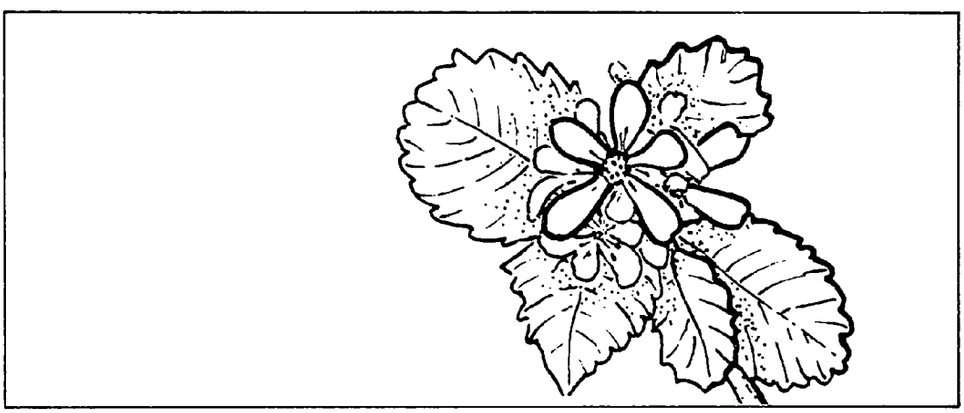

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