

NATURAL REVEGETATION OF ABANDONED CROP LAND IN THE PONDEROSA PINE ZONE OF THE PIKE'S PEAK REGION IN COLORADO

W. M. JOHNSON

*Rocky Mountain Forest and Range Experiment Station*¹

Cultivation in the ponderosa pine zone of Colorado has, in many instances, been unprofitable because of the uncertainty of crops and eventual loss of soil fertility. Consequently, many areas have been abandoned, and natural revegetation has resulted in the presence of all stages of the secondary succession, from the initial invasion to almost complete return to the original subclimax grassland community. Some of the more recently abandoned fields have been protected from grazing, while others have been grazed at different rates and different seasons of the year. Therefore, areas representing different periods of abandonment and different types of grazing use are available in the Pike's Peak region for the reconstruction of the abandoned field sere in the ponderosa pine-Douglas fir association.

Previous investigations of the rate and manner in which abandoned farm lands in the ponderosa pine zone revert to natural cover are not abundant. Hanson ('24) discussed briefly the secondary succession on abandoned fields in the ponderosa pine zone of northeastern Arizona. He described a first weed stage (*Verbesina-Amaranthus* associates), a second weed stage (*Senecio-Eriogonum* associates), a first grass stage (*Bouteloua-Agropyron* associates), and a subclimax grass stage (*Festuca-Muhlenbergia-Blepharoneuron* associates). In some instances the subclimax grass stage was omitted, and the succession passed directly from the first grass stage to the ponderosa pine climax. Shantz ('11), and Savage and Runyon ('37) discussed various aspects of the succession that occurs on abandoned farm

lands in the central and southern Great Plains. Similar discussions for other areas have been presented by Booth ('41) for Kansas and Oklahoma; Whitman, Hanson, and Loder ('43) for western North Dakota, and Costello ('44) for northeastern Colorado. In general, on the areas where these investigators have worked, there are four distinct associates, beginning with an annual weed type and progressing upward through perennial forb, mixed grass and forb, and, usually, a subclimax grass type—all preceding the final or climax association.

Other factors affecting the rate of revegetation of abandoned farm lands have been discussed by various workers. Runyon ('36) evaluated the distribution of the seed supply, Booth ('41) the effect of cultural methods and burning, and Weaver and Albertson ('40) the effects of drought.

The present study was made to determine, insofar as possible, the rate of revegetation and the stages of secondary succession on abandoned farm lands in the vicinity of the Manitou Experimental Forest² near Woodland Park, Colorado. Detailed studies of ten fields in various stages of succession were initiated in 1936 and were concluded in 1944. The development of the vegetation has been traced only from the initial invasion to the subclimax grass community. It is recognized that the ponderosa pine-Douglas fir association is the potential climax of this area and that the subclimax grass community may eventually be replaced by the conifers.

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² An experimental area operated by the Rocky Mountain Forest and Range Experiment Station, Forest Service, in cooperation with Colorado College, Colorado Springs, Colorado.

DESCRIPTION OF THE AREA

The ponderosa pine zone occurs generally at elevations from 6000 to 9000 feet throughout the Front Range of the Colorado Rockies. The topography is typically rough mountainous. *Pseudotsuga taxifolia*³ occurs commonly on the north slopes, while *Pinus ponderosa* is confined more generally to the drier south exposures and more level lands of the valleys. Numerous grassy parks varying in size from one to many acres are scattered throughout the zone. Farming is confined largely to these open parks, although in some instances the pine lands have been cleared and placed in cultivation. The common crops are potatoes and oats, but winter wheat, rye, and head lettuce are also raised to some extent. The Manitou Experimental Forest is centrally located within this zone and is typical of much of the Front Range area.

The soils in the vicinity of the Manitou Experimental Forest are derived chiefly from the Pike's Peak granite, but remnants of limestone and sandstone formations have contributed some of the finer soil particles. The soils are highly erodible, very porous, and of coarse texture.

Precipitation averages about 18 inches per year and occurs largely in the form of rains, with approximately three-fourths of the total moisture falling between April 1 and September 30. The winters are usually open but cold. Occasionally heavy snows occur in late spring (April or May). Drought years are not uncommon; during 1939 the total annual rainfall amounted to 7.99 inches.

METHODS

Species density and composition were determined by the "point observation"

³ Scientific names in general follow the nomenclature of A. S. Hitchcock, *Manual of Grasses of the United States*; and T. H. Kearney and Robert H. Peebles, *Flowering Plants and Ferns of Arizona*. Recent changes and segregations within certain genera, however, have been observed.

method (Stewart and Hutchings, '36). During the period of study approximately 300 sample plots were taken at random in fields representing periods of abandonment of three months to sixty-two years. Grazing use of these areas included complete protection, light winter use, and heavy summer use. Complete records were obtained from landowners regarding the periods of cultivation, types of crops raised, and the number of years the fields had been abandoned. Photographs were taken to show typical stages in the succession and the effects of erosion and of grazing use.

Detailed observations of density and composition of the plant cover were obtained first in 1936. The areas were re-examined at yearly intervals until 1940 and at irregular intervals until 1944. The data were compiled by periods of abandonment and by types of grazing use. The order of development of the different plant communities was then determined by the methods of inference and sequence (Clements, '28). Fortunately, there was enough overlapping of periods of abandonment and of successional stages so that reliable evidence was available to determine the sequence of development.

TRENDS OF SUCCESSION

Initial stage

Invasion by annual forbs is the first step in the natural recovery of plowed fields after the abandonment of cultivation. The cover, which is rapidly established in this initial stage, is variable and depends upon seed source, time of invasion, nature of the previous cultivated crop, and methods of cultivation. Occasionally nearly pure stands of *Setaria viridis* may occur as the initial stage or may follow, in the second year, a previous cover of annual forbs. *Setaria viridis* occurs most frequently on fields that had been in crops requiring periodic cultivation, such as potatoes or lettuce. More frequently, stands of *Chenopodium album*

and *Helianthus annuus* may occur to the virtual exclusion of all other species—most commonly on fields that had been in small grain crops. Other annuals, such as *Amaranthus retroflexus*, *Solanum nigrum*, *Helianthus petiolaris*, *Polygonum convolvulus*, and *Physalis pubescens*, may dominate the initial stage. These species are most commonly found in mixed stands.

In one field, representative of the earliest type of invasion (cultivated in the spring but not seeded to crops), the cover consisted primarily of three species: *Amaranthus retroflexus*, *Solanum nigrum*, and *Verbesina encelioides*. These three species occurred on all of the sample plots and made up 87.5 per cent of the composition (table I, fig. 1). Numerous other forbs were present but none contributed appreciably to the density or



FIG. 1. Annual weed stage on a field cultivated in the spring but not seeded to crops. A later stage in the succession may be seen in the left center.

TABLE I. Composition of annual weed stage on a field abandoned three months

Species	Fre- quency*	Density	Compo- sition†
per cent			
Grasses			
<i>Agropyron repens</i>	10	T‡	T
<i>Hordeum nodosum</i>	10	T	T
<i>Munroa squarrosa</i>	30	.10	.4
<i>Setaria viridis</i>	10	T	T
<i>Sitanion hystrix</i>	20	T	T
Subtotal		.10	.4
Forbs			
<i>Amaranthus retroflexus</i>	100	5.40	23.8
<i>Ambrosia trifida</i>	10	.75	3.3
<i>Chenopodium album</i>	50	.10	.4
<i>Cirsium ochrocentrum</i>	10	.03	.1
<i>Euphorbia</i> sp.	10	.15	.7
<i>Helianthus annuus</i>	20	.43	1.9
<i>Lactuca pulchella</i>	30	.60	2.6
<i>Lappula redowskii</i>	10	T	T
<i>Phacelia neomexicana</i>	50	.50	2.2
<i>Physalis pubescens</i>	10	.05	.2
<i>Polygonum aviculare</i>	40	.15	.7
<i>P. convolvulus</i>	10	T	T
<i>Solanum nigrum</i>	100	9.60	42.5
<i>Verbesina encelioides</i>	100	4.80	21.2
Subtotal		22.56	99.6
Total		22.66	100.0

* Based on square-foot-density plots of 100 square feet in area.

† Composition based on density.

‡ Trace—insufficient surface covered to warrant numerical density value.

composition. Four species are worthy of comment, however, because they were almost constantly present in the sere: *Chenopodium album*, *Euphorbia* sp., *Cirsium ochrocentrum*, and *Polygonum aviculare*. These species never become conspicuous in either frequency or density but they were usually present, even in the subclimax grass community. On this area forbs comprised 99.6 per cent of the total cover, with grasses making up the remainder. Of these, *Munroa squarrosa* was the only one that occurred in sufficient abundance to record as density. It was found on 30 per cent of the plots. *Sitanion hystrix*, another species commonly present throughout the sere, occurred on 20 per cent of the plots but not in sufficient quantity to record as density.

This initial stage of succession, irrespective of the composition, has little economic value and does not protect the soil from washing. The dense cover may reduce the compacting effects of

pounding rains, but, because of inadequate root systems and lack of organic debris, it is unable to bind the soil in place.

The annual weed stage is commonly of short duration because the soil usually retains enough fertility to favor the germination and development of perennial species. If normal weather conditions exist, the latter type of vegetation may become established during the second or third year after the field has been abandoned, but scanty rainfall or the loss of soil fertility through sheet erosion favors the continuation of the initial vegetation. Development of the second stage occurs as a result of the invasion of perennial species in increasing abundance. Some of the annual species are unable to withstand the resulting competition and disappear, but others remain throughout the succession and are still present, although much reduced in vigor and abundance, in the subclimax grass community.

Perennial forb stage

Within three to five years after the cessation of cultivation most fields are completely dominated by a stand of perennials which is both complex and variable. Density is perhaps more variable than composition—a range from 2 to 20 per cent ground cover being fairly common. Most of the vegetation consists of perennial forbs, but perennial grasses and shrubs are also present. Some annuals, principally *Chenopodium album*, *Helianthus petiolaris*, and *Euphorbia* spp. are present, but the luxuriant growth characteristic of these species in the annual weed stage is usually lacking.

Among the perennial forbs distinct colonization is typical (fig. 2). *Penstemon unilateralis* and *Linaria vulgaris* are the most conspicuous dominants. These species, in combination with *Erigeron flagellaris*, *Schedonnardus paniculatus*, and others, often form dense colonies, giving a flower garden aspect to the area. This colonization occurs early in the de-



FIG. 2. Mixed perennial weed stage on a field abandoned seven years. Distinct colonization is typical of this stage of development.

velopment of the perennial forb stage and is usually short-lived. The colonies are invaded by other forbs or grasses, and the aspect rapidly changes to that of the typical mixed forb cover.

Perennial grasses, such as *Agropyron smithii*, *A. trachycaulum*, *Bouteloua gracilis*, and *Muhlenbergia montana*, may be present at this stage but are usually inconspicuous and do not contribute greatly to the density of the cover (table II).

Among the grasses the early appearance of *Muhlenbergia montana* is worthy of note because it is a component of the climax association. At this stage of the sere it is of low frequency and contributes little to the composition. *Schedonnardus paniculatus* is the major grass component. It occurred on all of the plots, had an average density of 0.35 per cent, and comprised 9.4 per cent of the total composition or 50 per cent of the total grasses. Under grazing pressure it may be the only grass to remain in the stand. The appearance of *Stipa robusta* foretells the next stage in the succession.

Among the annual forbs *Chenopodium album*, *Helianthus petiolaris*, *Oenothera coronopifolia*, and *Polygonum aviculare* are the most common. These species made up 13.1 per cent of the total composition. The perennial forbs include *Astragalus goniatus*, *Chrysopsis villosa*, *Cirsium ochrocentrum*, *Erigeron flagellaris*, *Taraxacum officinale*, and *Potentilla glandulosa*. Among these, *Erigeron flagellaris* is perhaps the most important because of its persistence under grazing pressure, its ability to bind and hold the soil against erosive forces, and its durability throughout the succession.

Only two species of shrubs were recorded for this field. *Artemisia dracunculoides* is of minor importance, but *A. frigida* plays a major part in the successional development. The latter species is usually frequent and its density is largely determined by grazing pressure. *Rosa arkansana* did not appear on this field but it is frequently abundant in this stage.

TABLE II. *Composition of perennial weed stage on a field abandoned five years*

Species	Frequency	Density	Composition
per cent			
Grasses			
<i>Hordeum jubatum</i>	20	.02	0.5
<i>Muhlenbergia montana</i>	20	.05	1.4
<i>Schedonnardus paniculatus</i>	100	.35	9.4
<i>Stipa robusta</i>	70	.28	7.6
Subtotal		.70	18.9
Forbs			
<i>Astragalus goniatus</i>	70	.22	5.9
<i>Chenopodium album</i>	90	T	T
<i>Chrysopsis villosa</i>	30	.08	2.2
<i>Cirsium ochrocentrum</i>	40	.50	13.5
<i>Erigeron flagellaris</i>	90	.72	19.4
<i>Helianthus petiolaris</i>	90	.15	4.0
<i>Oenothera coronopifolia</i>	90	.12	3.2
<i>Polygonum aviculare</i>	60	.22	5.9
<i>Potentilla glandulosa</i>	40	.08	2.2
<i>Taraxacum officinale</i>	20	T	T
Subtotal		2.09	56.3
Shrubs			
<i>Artemisia dracunculoides</i>	40	.10	2.7
<i>A. frigida</i>	90	.82	22.1
Subtotal		.92	24.8
Total		3.71	100.0

Seedlings of the climax dominants, *Pinus ponderosa* and *Pseudotsuga taxifolia*, occur frequently in the perennial forb stage. The limited mobility of the seeds of these trees results most frequently in aggregation around boundaries of the fields in the zone of contact with the climax. Occasionally, however, migrules may become established at considerable distances from the parent plants. Seedlings are apparently more readily established and more abundant on those portions of abandoned fields that were originally covered by these trees than on adjacent areas where only the subclimax grass community had existed prior to cultivation.

The perennial forb stage is of relatively short duration. Perennial grasses usually become established and replace many of the perennial weeds within seven to ten years after abandonment of cultivation. Under grazing pressure,

however, a cover of *Artemisia frigida*, *Erigeron flagellaris*, and *Schedonnardus paniculatus* may persist indefinitely.

Mixed grass and weed stage

Stipa-Agropyron phase. The perennial forb stage is replaced by a mixed grass and weed community. The early phase is characterized by a mixture of *Stipa robusta*, *S. viridula*, and *Agropyron trachycaulum* in about equal abundance, with the *Stipas* occupying the drier sites and the *Agropyron* occurring more abundantly on the wetter soils in small depressions (fig. 3). A gradual transition, however, results in the replacement of *Agropyron* by *Bouteloua gracilis* and *B. hirsuta*, although *Stipa* remains and may dominate the vegetation.

The development of the *Stipa-Agropyron* phase under protection from grazing is characterized by a great increase in number of both grass and forb species (table III), and by the replacement of the forb aspect by a grass aspect. Most of the grass species that were present in



FIG. 3. A *Stipa-Agropyron* community in a field abandoned 15 years and protected from grazing for 12 years.

TABLE III. Composition of mixed grass and weed stage on a field abandoned ten years

Species	Frequency	Density	Composition
per cent			
Grasses			
<i>Agropyron smithii</i>	15	T	T
<i>A. trachycaulum</i>	35	.17	1.0
<i>A. subsecundum</i>	10	.02	.1
<i>Bouteloua gracilis</i>	5	T	T
<i>Koeleria cristata</i>	5	.01	.1
<i>Muhlenbergia montana</i>	20	.21	1.3
<i>Poa pratensis</i>	5	.01	.1
<i>Schedonnardus</i>			
<i>paniculatus</i>	30	.08	.5
<i>Sitanion hystrix</i>	75	.48	3.0
<i>Stipa robusta</i>	40	.22	1.4
<i>S. viridula</i>	40	.21	1.3
Subtotal		1.41	8.8
Forbs			
<i>Aster</i> spp.	15	.05	.3
<i>Astragalus goniatus</i>	60	.40	2.5
<i>Chamaerhodos nuttallii</i>	20	.06	.4
<i>Chenopodium album</i>	75	.02	.1
<i>Chrysopsis villosa</i>	15	.14	.9
<i>Cirsium ochrocentrum</i>	65	.16	1.0
<i>Erigeron flagellaris</i>	80	4.59	28.6
<i>Euphorbia</i> sp.	20	.01	.1
<i>Helianthus annuus</i>	15	.02	.1
<i>H. petiolaris</i>	85	.14	.9
<i>Lappula occidentalis</i>	45	.01	.1
<i>Lepidium densiflorum</i>	50	.09	.6
<i>Oenothera coronopifolia</i>	100	.71	4.4
<i>Oxytropis lambertii</i>	10	.11	.7
<i>Penstemon unilateralis</i>	20	.01	.1
<i>Polygonum aviculare</i>	50	.02	.1
<i>P. convolvulus</i>	65	.06	.4
<i>Potentilla glandulosa</i>	55	.30	1.9
<i>Senecio eremophilus</i>	15	.01	.1
<i>S. fendleri</i>	50	.04	.3
<i>Solanum nigrum</i>	20	.02	.1
<i>Taraxacum officinale</i>	35	.16	1.0
<i>Tragopogon parvifolius</i>	10	.02	.1
Subtotal		7.15	44.8
Shrubs			
<i>Artemisia frigida</i>	95	6.40	40.1
<i>Rosa arkansana</i>	30	1.01	6.3
Subtotal		7.41	46.4
Total		15.97	100.0

the perennial forb stage remain and usually increase in abundance. *Muhlenbergia montana* and *Agropyron smithii* are typical examples. In addition, *Koeleria cristata*, *Poa pratensis*, *Agrostis hiemalis*, and *Bromus anomalus* frequently become established and usually remain throughout the succession. This development of grasses is seriously re-

tarded by grazing. It is not at all uncommon to find fields that have been abandoned from twenty to thirty years on which, as a result of grazing use, *Schedonnardus paniculatus* is the principal or only grass species present. Either *Stipa robusta* or *Sporobolus cryptandrus* may take the place of *Schedonnardus* under these conditions. Sometimes all three species may be found together. With the exception of *Agropyron smithii*, the wheatgrasses (*A. trachycaulum* and *A. subsecundum*) usually disappear before the subclimax grass stage is reached. *Stipa robusta* and *S. viridula* are usually long-lived members of the community and are not replaced until the subclimax grass stage is nearing its maximum development. *Bouteloua gracilis* makes its appearance in this stage. In later phases it may become the principal grass and occur in almost pure stands.

The number of forb species in this phase is large and variable from place to place. Most of them remain throughout the succession, but as the association develops the forb density is much reduced. *Erigeron flagellaris* is usually the most abundant species. *Helianthus annuus* and *Solanum nigrum* are usually present as remnants of the initial weed stage but seldom remain beyond the early development of the mixed grass and weed community.

Artemisia frigida and *Rosa arkansana* are the only two shrub species of any importance occurring in the succession. In this stage *Artemisia frigida* is usually present in great abundance. It is relatively unpalatable to cattle and will increase rapidly under grazing pressure, but *Rosa arkansana* is palatable and is either entirely removed or much reduced in stature and vigor if the grazing use is heavy.

This early phase of the mixed grass and weed stage may be of relatively short duration, approximately ten years, if the succession is not retarded by overgrazing.

Stipa-Bouteloua phase. This late phase

of the mixed grass and weed community will probably develop within fifteen to twenty-five years after cessation of cultivation, if grazing use is restricted. Unfortunately, no abandoned fields were available for study which had been protected from grazing long enough for this phase to develop under natural conditions. On grazed fields the *Stipa-Bouteloua* phase was well developed fifty-six years after cultivation had stopped. The area shown in figure 4 had been abandoned sixty-two years and is representative of the late transition to the subclimax grass community.

In this phase the grass species have further increased in density and comprise a much larger proportion of the total population. Within this group the principal changes consist of an increased density of *Bouteloua* and *Muhlenbergia* (table IV), and of the introduction of two more of the climax species, *Festuca arizonica* and *Carex stenophylla*.



FIG. 4. The transition into a subclimax grass community on a field abandoned 62 years and subjected to grazing use. *Bouteloua gracilis* is replacing the *Stipa-Agropyron* community and in turn is being invaded by the climax grasses *Muhlenbergia montana* and *Festuca arizonica*.

TABLE IV. *Composition of the early subclimax grass stage on a field abandoned 62 years*

Species	Frequency	Density	Composition
		per cent	
Grasses and sedges			
<i>Agropyron smithii</i>	62	.12	.7
<i>Bouteloua gracilis</i>	100	4.11	23.9
<i>Festuca arizonica</i>	67	.69	4.0
<i>Koeleria cristata</i>	19	.01	.1
<i>Muhlenbergia filiculmis</i>	5	.01	.1
<i>M. montana</i>	86	2.16	12.6
<i>Schedonnardus</i>			
<i>paniculatus</i>	5	.02	.1
<i>Sitanion hystrix</i>	90	.10	.6
<i>Stipa comata</i>	67	.07	.4
<i>S. robusta</i>	71	.38	2.2
<i>S. viridula</i>	86	.33	1.9
<i>Carex stenophylla</i>	52	.20	1.2
Subtotal.		8.20	47.8
Forbs			
<i>Achillea lanulosa</i>	29	.07	.4
<i>Allium acuminatum</i>	62	.02	.1
<i>Antennaria aprica</i>	76	1.70	9.9
<i>Astragalus goniatius</i>	71	.29	1.6
<i>Calochortus gunnisonii</i>	5	T	T
<i>Castilleja integra</i>	5	T	T
<i>Chenopodium album</i>	100	.01	.1
<i>Chrysopsis villosa</i>	86	.30	1.7
<i>Cirsium ochrocentrum</i>	52	.08	.5
<i>Cryptantha thyrsiflora</i>	5	.01	.1
<i>Erigeron canadensis</i>	5	T	T
<i>E. flagellaris</i>	90	.78	4.5
<i>Eriogonum alatum</i>	14	.01	.1
<i>Euphorbia</i> sp.	5	.01	.1
<i>Geranium fremontii</i>	38	.01	.1
<i>Lappula occidentalis</i>	33	.03	.1
<i>Linum lewisii</i>	5	.01	.1
<i>Lupinus argenteus</i>	33	.10	.6
<i>Lygodesmia juncea</i>	5	T	T
<i>Mertensia lanceolata</i>	19	T	T
<i>Oenothera coronopifolia</i>	90	.13	.8
<i>Orthocarpus luteus</i>	48	.03	.1
<i>Oxytropis lambertii</i>	14	.05	.3
<i>Penstemon unilateralis</i>	14	T	T
<i>Polygonum aviculare</i>	95	.17	1.0
<i>Potentilla effusa</i>	24	.13	.8
<i>P. glandulosa</i>	81	.06	.3
<i>Senecio fendleri</i>	95	.33	1.9
<i>Taraxacum officinale</i>	14	.01	.1
<i>Tragopogon parvifolius</i>	10	T	T
Subtotal.		4.34	25.3
Shrubs			
<i>Artemisia frigida</i>	100	4.58	26.7
<i>Mamillaria vivipara</i>	10	.01	.1
<i>Rosa arkansana</i>	10	.01	.1
Subtotal.		4.60	26.9
Total.		17.14	100.0

Many climax forb species become established in this stage. *Achillea lanulosa*, *Antennaria aprica*, *Geranium fre-*

montii, *Oxytropis lambertii*, and *Senecio fendleri* are usually the most abundant.

In spite of the greater number of species the total density of the forbs is lower than in the preceding perennial forb stage, and they make up a smaller proportion of the total cover. *Erigeron flagellaris* is still present but is much reduced in abundance. Individual plants of this species are numerous but are depauperate specimens lacking the vigor and size common in the earlier stages of succession.

Artemisia frigida is still the principal shrubby species but is reduced in density. *Rosa arkansana* is usually present, but only in limited quantities. *Mamillaria vivipara*, the only member of the cactus family in this area, may be present in limited quantity and remain in the climax association.

FACTORS AFFECTING SUCCESSION

Weather

In the Pike's Peak area climatic factors usually favor relatively rapid plant succession. Warm summers and adequate rainfall during the growing season encourage vigorous growth and the production of large quantities of seed. The establishment of seedlings is sometimes inhibited, however, by lack of moisture during June; otherwise, the rainfall is well distributed throughout the growing season.

Droughts are usually not as injurious to plant succession as they are in other areas such as the Great Plains. Most of the annual rainfall occurs during the summer months. In 1939, the driest year on record at the Manitou Experimental Forest, the total annual rainfall was only 7.99 inches, but 5.68 inches fell during the growing season from April to September. Dry years are more severe on forbs than on grasses. At such times the blossoming of the forbs is much reduced, but the grasses, especially the bunchgrasses, almost invariably produce seed stalks.



FIG. 5. Abandoned fields are easily eroded and where the top soil has been removed succession is retarded.

Erosion and runoff

As soon as the initial porosity of the soil has been lost through compaction, the abandoned fields in the Pike's Peak area are subject to severe sheet and gully erosion (fig. 5). Johnson and Niederhof ('41) have shown that surface runoff was 20-25 per cent greater from abandoned fields than from adjoining native grassland and that erosion was 159-260 per cent greater. These factors play an important part in succession. In almost any field various stages of development can be found which are directly associated with the amount and kind of erosion that has occurred. For example, a field in the mixed grass and weed stage may contain areas in the initial or early perennial forb stage. Upon examination it is usually evident that sheet erosion has been severe on these areas and that the finer soil particles have been removed, leaving a soil so coarse and sterile that the rate of succession has been retarded. On such areas *Erigeron flagel-*

laris, *Polygonum aviculare*, *P. convolvulus*, and *Artemisia frigida* may be the only plants able to survive the existing conditions. Again *Agropyron smithii*, *A. trachycaulum*, and *A. subsecundum* may be entirely lacking from the early phase of the mixed grass and weed stage because gullying has occurred in the swales and has prevented the accumulation of sufficient moisture to enable these plants to survive.

Grazing

The degree of grazing pressure to which an area has been subjected is equally as important as erosion and runoff in its effect on plant succession. Regardless of the stage attained, too heavy grazing use will either maintain or reduce the composition to a stand in which *Artemisia frigida* is the dominant species (fig. 6). Associated with it may be *Erigeron flagellaris* and *Schedonnardus paniculatus*, to the almost complete exclusion of all other plants. *Sporobolus*



FIG. 6. Grazing use may perpetuate a stand of *Erigeron flagellaris*, *Polygonum aviculare*, and *Artemisia frigida*. Photographs represent portions of the same field: left, protected from grazing; right, grazed heavily during summer months.

cryptandrus may develop on some areas but it is infrequent. Occasionally, if the succession has reached the *Stipa-Bouteloua* stage, *Stipa robusta* may be maintained in sufficient abundance to lend aspect to the area. This usually indicates that the grazing pressure is somewhat lighter or that the heavy pressure has been applied only for a relatively short period.

Reseeding

Some fields in this area have been revegetated artificially in order to hasten their return to forage production. The species most commonly used for reseeding are crested wheatgrass (*Agropyron cristatum*), smooth brome (*Bromus inermis*), and yellow sweetclover (*Melilotus officinalis*). Crested wheatgrass is used most frequently, and good stands have been obtained. Many trials with this species were apparently failures the first season but later developed into healthy stands. Good stands are usually obtained within two or three years.

Smooth brome has also been successfully used. A 1-acre plot planted during the 1939 drought had developed into a good stand by 1940. In 1944 it was still in good condition, even though it had been heavily grazed each winter. Yellow sweetclover planted in the fall of 1936 made excellent growth during 1937 and 1938, but since that time has become much reduced in density and vigor, largely the result of competition from other species.

The effects of artificial reseeding on secondary succession on abandoned fields are not too well known. Shantz ('40), in discussing artificial revegetation, has stated that "Often the re-establishment of the natural grass, brush, or forest cover is delayed in proportion as a temporary success is secured by the use of introduced species." Limited observations on reseeded areas near the Manitou Experimental Forest indicate that the secondary succession on such areas may begin with the *Stipa-Bouteloua* stage. *Muhlenbergia montana* is also a common

invader of reseeded fields. Regardless of the effect on the succession, successful reseeding to adapted species will provide a cover of vegetation that will stabilize the soil more quickly than is usually achieved through natural development.

DISCUSSION

There has been insufficient study of other areas in the ponderosa pine region to reveal adequately the general sequence in secondary succession on abandoned fields. In the Pike's Peak region, however, the stages of succession appear to follow closely those which have been determined for other areas. The principal trends that have been observed are: (1) an initial invasion of annual forbs with high densities of relatively few species; (2) the replacement of this stage by one in which perennial forbs are dominant but total densities are usually much reduced; (3) the invasion of perennial grasses in increasing abundance; and (4) the increased numbers and density of permanent members of the community as the climax is approached. Some of the climax grasses, such as *Muhlenbergia montana*, appear early in the succession and persist throughout the development. Other species, such as *Festuca arizonica*, generally fail to appear until the transition to the subclimax grass phase is approached.

Although many factors may affect the rate and type of the succession, the two best known and most influential in the Pike's Peak area are erosion and grazing pressure. In many cases the failure of any one stage to develop, or to progress into the next higher stage as rapidly as it should, may be traceable directly to the effects of erosion. The coarse, highly erodible, granitic soils may become so deficient in both fertility and available moisture that succession is halted or greatly retarded. Because of its wide occurrence sheet erosion may be of greater importance than gully erosion.

The knolls in many fields are barren of vegetation because the finer soil particles have been removed, and plants can no longer obtain sufficient moisture or nutrients for growth. Gully erosion is more spectacular and perhaps equally damaging in its widespread effect on water yields and watershed management but probably has less effect on the rate of succession because of its limited extent. Its greatest effect is probably in the reduction or elimination of the initial phase of the mixed grass and weed associates, where wheatgrasses are unable to survive because of the lowered moisture content resulting from gullying.

The effect of grazing on secondary succession is similar to that of erosion in that succession may be halted at any stage. The principal difference, however, is that under grazing pressure stands containing only unpalatable species will develop and maintain themselves until grazing management is changed. *Artemisia frigida* is universal throughout the zone as a species that will maintain itself under grazing pressure. This species, in combination with *Schedonnardus paniculatus*, *Stipa robusta*, *Erigeron flagellaris*, *Chrysopsis villosa*, and others, comprises the vegetation on abandoned fields which have been heavily grazed.

If livestock are allowed free access to abandoned fields in connection with other pasture, considerable concentration will occur because of the numerous palatable plants that are present. This may be responsible for retardation or even stagnation of the succession. These grazing coactions are not as pronounced if the fields are used carefully during the late fall or early winter months after the vegetation has matured. Fields that have been grazed only during this period show very little retardation in rate of succession.

SUMMARY

Secondary succession on abandoned fields in the ponderosa pine zone in the

vicinity of Pike's Peak, Colorado, progresses through the following stages:

1. An annual weed stage characterized by a few species occurring in great abundance, such as *Chenopodium album*, *Solanum nigrum*, *Amaranthus retroflexus*, *Verbesina encelioides*, and *Setaria viridis*. Occasionally almost pure stands of either one or two species may develop. The annual forb stage is of short duration, usually only one or two years.

2. A perennial forb stage characterized by an increased number of perennial grasses and forbs but having lower total densities of plant cover. *Agropyron smithii* and *Muhlenbergia montana*, as well as some of the permanent forb species, *Cirsium ochrocentrum*, *Erigeron flagellaris*, and *Astragalus goniatus*, make their appearance in this stage and become permanent members of the subclimax. This stage may last from 7 to 10 years.

3. A mixed grass and forb stage which, in the early period of development, is characterized by an abundance of *Stipa robusta* and *Agropyron pauciflorum*. *Bouteloua gracilis* gradually replaces the *Agropyron* in the later phase. Perennial forbs increase both in numbers and abundance. The stage may last from 10 to 25 years.

4. The subclimax bunchgrass stage in which *Muhlenbergia montana* and *Festuca arizonica* are the dominant species.

5. The climax *Pinus ponderosa*-*Pseudotsuga taxifolia* association.

Grazing pressure and loss of soil moisture and fertility from erosive action are the principal factors affecting succession. Grazing pressure may maintain a stand

of *Artemisia frigida* and other unpalatable species indefinitely.

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