

———. 1958b. Summary and interpretation of underground development in natural grassland communities. *Ecol. Monographs* 28: 55-78.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. *Ecology* 43: 125-129.

ROOT DEVELOPMENT OF NATIVE PLANTS UNDER THREE GRAZING INTENSITIES¹

JOSEPH L. SCHUSTER²

*Southern Forest Experiment Station, U.S. Forest Service
Nacogdoches, Texas*

The purpose of this study was to determine the effects of various intensities of grazing upon roots and root systems of plants native to the ponderosa pine zone of the Colorado Front Range. It was designed to ascertain the root characteristics of certain species of the plant community and any changes in root distribution induced by 17 years of moderate and heavy grazing by cattle. The cumulative effects of such grazing are also illustrated.

Most studies concerning the effects of plant defoliation show that any cropping (clipping or grazing) reduces plant growth, especially root growth. The initial root and rhizome response to defoliation is the cessation of elongation (Parker and Sampson 1931, Crider 1955). Subsequent reactions to continued defoliation are reduction in root numbers and branching (Jacques 1937, Albertson, Riegel, and Launchbaugh 1953), root diameter (Biswell and Weaver 1933), and depth of soil penetration (Ruby and Young 1953, Cook, Stoddart, and Kinsinger 1958). The amount of reduction is directly related to the severity and frequency of defoliation (Graber 1931, Albertson et al. 1953, Thaine 1954). In general the degree of defoliation is more detrimental to root growth than frequency of defoliation. Crider (1955) showed that apical growth of grass roots stopped within 24 hr after the removal of 40% or more of the foliage in one operation. The time required for roots to resume growth varied directly with the degree of foliage removal.

The consequences of overgrazing are apparently carried over from season to season. Weaver

(1950) and Tomanek and Albertson (1957) found that continued overgrazing not only reduces the number, size, and extent of underground parts of the individual plants, but also brings about changes in species composition, from tall grasses to short grass.

STUDY AREA

The study area was a typical ponderosa pine-bunchgrass range located on the Manitou Experimental Forest, 28 miles northwest of Colorado Springs, Colorado. It has a gentle east-facing slope (20% or less) with low ridges that run east and west. Elevations range from 7,600 ft on the east to 8,200 ft on the west. Cold winters with little snow and mild summers prevail. Annual precipitation has ranged from 8 to 23.5 in., and averages 15.3 in. Three-fourths of the yearly precipitation falls as rain from April through September.

Surface soils, normally about 12 to 18 in. deep, are reddish brown, sandy loams or loams, low in organic matter, and slightly acid. Subsoils are mostly sandy loams or sandy clay loams that grade into the unconsolidated gravelly parent material at varying depths of 10 to 62 in.

Four vegetation types occur on the experimental area (Johnson 1953): grassland parks, open timber, dense timber, and abandoned fields. Ponderosa pine (*Pinus ponderosa* Lawson) is dominant in the overstory. The most important forage species are mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.) and Arizona fescue (*Festuca arizonica* Vasey). Other species of importance are blue grama (*Bouteloua gracilis* (H.B.K.) Lag.), sedges (*Carex* spp.), fringed sagebrush (*Artemisia frigida* Willd.), Rocky Mountain pussytoes (*Antennaria aprica* Greene), cinquefoil (*Potentilla* spp.), and Fendler sandwort (*Arenaria fendleri* A. Gray). Mountain muhly and Arizona fescue produced the most cover in ungrazed enclosures and progressively less on moderately and heavily grazed ranges. In contrast, the cover of less desirable species such as Rocky Mountain pussytoes was as much or greater in heavily or

¹ Based on a thesis submitted to the Graduate School of Colorado State University, Fort Collins, Colorado. The investigation was cooperative between Colorado State University and the Rocky Mountain Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Fort Collins, Colorado.

² The author acknowledges the invaluable guidance and assistance of C. H. Wasser, Dean of the College of Forestry, Colorado State University, who supervised the study. Thanks are also due the members of my graduate committee: D. S. Romine, L. D. Love, D. R. Smith, F. C. Daugherty, and D. F. Hervey, and to personnel at the Manitou Experimental Forest who assisted with the field work.

moderately grazed ranges than in ungrazed exclosures. Fringed sagebrush produced similar amounts of cover on all ranges regardless of grazing treatment.

METHOD AND MATERIALS

The study was conducted on four native range pastures of which two had been grazed moderately and two heavily by yearling heifers each grazing season since 1943. Grazing was considered moderate where 30-40% of the herbage of the grasses and sedge palatable to cattle was utilized during a 5-month (June through October) grazing season. Utilization of 50% or more was considered heavy grazing; it varied considerably from year to year and in some years approached 75% herbage removal. The percentage utilization was estimated by measuring stubble heights of plants on the grazed areas and converting to herbage weight removal by use of established height-weight relationships. The pastures ranged from 251 to 289 acres. A 2-acre exclosure located in a grassland area of each pasture had received no cattle grazing since 1940. These exclosures represented the no-grazing treatment and were used as the basis for comparison of moderate and heavy grazing intensities.

Three sampling points were randomly located within grassland parks (Fig. 1) in each pasture. Additionally, two sample points were located in the exclosure of three of the pastures. Thus, each grazing intensity and no grazing was represented by six sampling points. A trench 4 ft wide, 7 ft deep, and 15 ft long was dug at each sample point. Species composition along one edge of the trench was determined by line intercept. Two root samples were excavated from the wall of each trench, totaling 12 samples from each grazing intensity. Effort was made to sample mountain muhly, Arizona fescue, blue grama, fringed sagebrush, and pussytoes in the relative proportions that they occurred along the trench wall.



FIG. 1. Grassland park representative of the sites from which samples were taken for study.



FIG. 2. Nail-board being inserted into trench wall for root-sample excavation.

The nail-boards were made of a $\frac{1}{2}$ -in. plywood board 24 in. wide and 36 in. long, with 3-in. steel sides along the two 36-in. edges and the bottom 24-in. edge. Sixteen-penny nails were inserted at 2-in. intervals through the back of the board and protruded into the frame $2\frac{3}{4}$ in. The nails and steel sides were held in place by a $\frac{1}{2}$ -in. plywood board bolted to the back of the frame. The inside dimensions of the nail-boards were 3 by 24 by 36 in. The frame was open on the face and the top 24-in. edge. A $\frac{1}{2}$ -in. mesh hardware cloth was inserted among the nails to help hold the roots in their natural positions. The cloth allowed water and soil to pass beneath exposed roots and minimized abrasion of roots by soil particles.

Root samples were excavated by pressing the nail-boards into the trench wall with jacks (Fig. 2) and slicing the enclosed soil monolith from the trench wall with a steel blade. One sample per trench was excavated to a 3-ft depth and the other to 6 ft by taking samples in two parts. The samples were soaked in water for at least 2 hours after which the soil was removed from the roots with a fine spray of water (Fig. 3).

The root samples were photographed and the 6-ft



FIG. 3. The washing process. The roots are lifted on the hardware cloth as the washing progresses to allow water and soil to pass under exposed roots.

sample from each trench was drawn to $\frac{1}{2}$ -in. scale in color. The photographs and drawings allowed visual comparisons of the root systems after disposition of the samples. Plants of mountain muhly, Arizona fescue, blue grama, fringed sagebrush, and pussytoes contained in the samples were measured individually in each sample. Maximum depth and maximum lateral root spread for each of these species and the number of roots (all species) extending below 1-ft depth levels were recorded. Six 1-ft depth sections were designated, beginning with the surface foot of soil and ending with the sixth (5 to 6 ft) level. Roots and rhizomes in each depth section were segregated into grasses (grass and grasslike) or nongrasses (forbs and shrubs) and weighed to the nearest 0.1 gm (air-dry).

Variance analyses were used to examine variations in species lateral root spread and rooting depth. Differences in total, grass, and nongrass root weights between species grazing intensity and soil depth levels were also tested. Individual comparisons were made of root characteristics of non-grazed versus heavily and moderately grazed areas, and moderately grazed versus heavily grazed areas. Differences, tested by the "F" test, are reported as not significant, significant (at the .05 level), or highly significant (at the .01 level).

Descriptions of the root systems of the individual species are based on the measurements and analysis described above, comparisons of photographs and drawings, and field observation during the study.

RESULTS

Vegetation cover and composition

Percentage composition of sample vegetation as determined from basal area intercept measurements of washed plants on the nail-boards was comparable to that obtained by line intercept along sample trenches. Mountain muhly, the most abun-

TABLE I. Percentage of average cover and botanical composition along sample trenches¹

Species	No grazing		Moderate grazing		Heavy grazing	
	Cover ²	Compo-sition	Cover	Compo-sition	Cover	Compo-sition
Mountain muhly.....	17.3	77.5	7.5	30.1	9.0	39.3
Arizona fescue.....	.9	4.0	1.5	6.3	.1	.7
Blue grama.....	1.7	7.4	10.1	40.7	7.2	31.6
Other grasses.....	1.0	4.4	1.4	5.6	.9	4.1
Fringed sagebrush.....	.8	3.7	2.5	9.9	1.5	6.3
Rocky Mountain pussytoes.....	.2	1.0	.8	3.1	2.8	12.4
Other forbs.....	.4	2.0	1.0	4.3	1.3	5.6
Total.....	22.3	100.0	24.8	100.0	22.8	100.0

¹Average of percentages of crown spread from six 15-ft line transects per grazing treatment.

²Percentage groundline intercept.

dant species in exclosures, was considerably less abundant in moderately grazed range (Table I). All other species had a higher percentage of ground cover (by intercept) and composition in moderately grazed areas than in exclosures. This was especially true with blue grama and fringed sagebrush, both of which in turn were then less abundant in heavily grazed pastures.

Arizona fescue was relatively more abundant and furnished a larger percentage of the grass cover in moderately grazed pastures than in exclosures, but it accounted for considerably less of the plant cover and composition in heavily grazed areas. In general, grasses were less abundant and furnished less cover on heavily grazed areas than

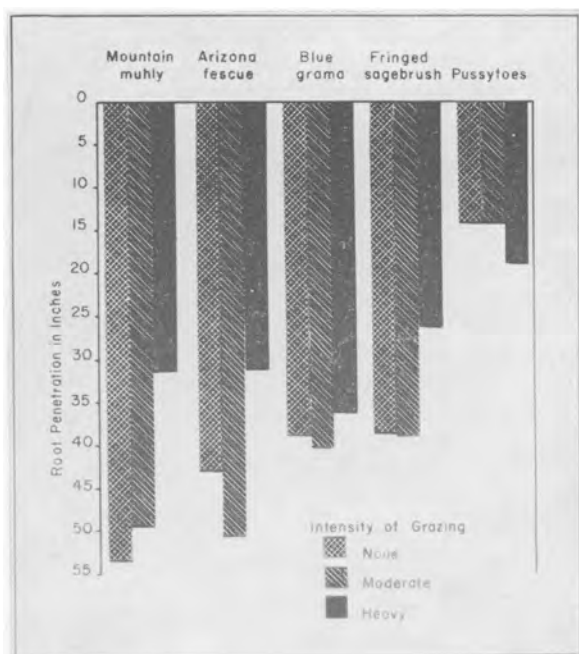


FIG. 4. Average maximum root penetration of five important species under three intensities of grazing.

on moderately grazed areas, while forbs tended to be more abundant in the heavily grazed pastures.

Root penetration

Roots penetrated as deeply in moderately grazed pastures as in ungrazed exclosures. With the exception of pussytoes, root extension for all species was significantly less in heavily grazed pastures than in moderately grazed or ungrazed areas (Fig. 4). Its greater depth of rooting in these pastures indicates that pussytoes thrived under heavy range use, presumably because the palatable species were being depressed by overgrazing.

The number of roots extending below the second foot of soil was similar in moderately and non-grazed areas, but was less under heavy use.

Lateral spread of roots

Lateral root spread of grasses, as measured from the center of the plant, was progressively less from no grazing to heavy grazing. Fringed sagebrush and pussytoes attained their widest lateral spread in moderately grazed pastures (Fig. 5). Differences in lateral root spread of the species between grazing intensities can possibly be attributed to cattle preference for grasses. Under moderate grazing, grasses received heavier relative use than the broadleaved species. The direct effect was to reduce lateral spread of grass root, thus permitting roots of the nongrasses to extend into areas previously occupied by grass roots. It was evident, however, that with continued heavy grazing some

of the less palatable plants were also detrimentally affected, resulting in an overall reduction in root systems of all species as measured by lateral spread.

Root weight

Both total root weight of all species combined and root weight of all grasses was significantly greater in ungrazed than in moderately or heavily grazed areas. Differences in root weights of non-grass plants between the areas were not significant.

Differences in root weight in the top 3-ft depth levels were highly significant, with significantly less being found with each 1-ft increase in depth. The most pronounced decrease in root weight occurred from the 1-ft to the 2-ft depth level. With but one exception (nongrasses, ungrazed), at least 78% of the total root weight was found in the upper foot of soil. This percentage was always above 80% for grasses and averaged as high as 86% for grasses under heavy stocking. The proportion of nongrass roots increased at greater depths, and nongrass roots actually outweighed grass roots in the lower three depth levels in heavily grazed pastures. Grasses made up 93% of all roots in exclosures, 90% in moderately grazed, and 81% in heavily grazed areas. The differences were brought about by the decrease in grass root weights and increase in nongrass root weights as grazing intensity increased (Table II).

Root characteristics of the individual species

Mountain muhly.—Mountain muhly in ungrazed conditions has an extensive fibrous root system. The heavily branched roots have a nonpersistent, white, flaky cortex. Roots originate from each plant tiller and spread obliquely in the top 3-6 in. of soil before descending vertically. Main roots branch and rebranch profusely to form a dense mat in the top 6 in. of soil. Laterals mingle with roots of nearby plants. Main roots support 15-20 branch rootlets per inch.

Roots in moderately grazed areas formed dense mats in the top 2-3 in. of soil. They spread obliquely in the top 3-6 in. of soil before growing vertically. The main roots had 10-15 branch rootlets per inch.

Roots from heavily grazed pastures had much smaller diameters and were more fragile than those from ungrazed areas. They formed a dense mat only in the top 2 in. of soil, with the lateral spread mostly restricted to the top 3 in. of soil.

Arizona fescue.—In ungrazed areas Arizona fescue has a dense, fibrous root system of tough, wiry, and strongly branched roots. The persistent cortex is light brown on young roots and dark brown on older roots. Root hairs are persistent. The roots originate from the base of the plants,

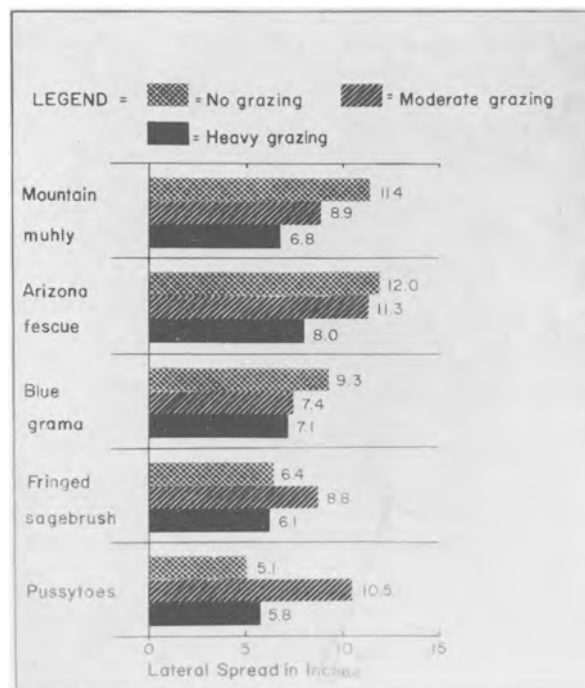


FIG. 5. Maximum lateral spread of roots under three intensities of grazing.

TABLE II. Average air-dry root weight per soil depth section (864 cu. in.) for various intensities of grazing¹

Grazing intensity and depth level (ft)	Grass roots		Nongrass roots	
	Grams	Percent-age	Grams	Percent-age
Ungrazed				
0-1	20.59	80.81	1.61	60.99
1-2	3.70	14.52	.59	22.35
2-3	.78	3.06	.21	7.95
3-4	.29	1.14	.16	6.06
4-5	.10	.39	.06	2.27
5-6	.02	.08	.01	.38
Total	25.48	100.0	2.64	100.0
Moderately grazed				
0-1	17.16	80.04	1.72	78.54
1-2	3.20	14.93	.28	12.78
2-3	.60	2.80	.11	5.02
3-4	.31	1.44	.07	3.20
4-5	.14	.65	.01	.46
5-6	.03	.14	0	0
Total	21.44	100.0	2.19	100.0
Heavily grazed				
0-1	13.04	86.30	3.04	77.55
1-2	1.78	11.78	.50	12.76
2-3	.24	1.59	.17	4.34
3-4	.04	.26	.08	2.04
4-5	.01	.07	.08	2.04
5-6	0	0	.05	1.27
Total	15.11	100.0	3.92	100.0

¹Average of 12 samples from each grazing intensity.

descend, and spread at a 45° angle. They reach an average maximum lateral spread about 12 in. deep before becoming vertical. Roots have relatively few branches near the surface but become more branched below a depth of 6 in.

Roots from moderately grazed pastures were tough and wiry but smaller and were slightly easier broken than those from ungrazed exclosures. The roots spread at a 45° angle from the plant base and reached maximum lateral spread (11 in.) at a depth of about 8 in. Roots of Arizona fescue sampled in heavily grazed pastures were small and had few branches. Lateral spread and depth of penetration was much less than in moderately grazed pastures or exclosures.

Blue grama.—Ungrazed blue grama has fine fibrous roots that originate from the plant base and tillers. They are heavily branched, very pale brown, and have a firm, usually persistent cortex. The main roots have many small rootlets (usually 25-30 per in.) approximately 1 in. in length. Average maximum lateral spread, most of which occurred in the top 2-3 in. of soil, was about 9 in. The exposed roots formed a dense, fine-rooted mat to about 6 in. Root numbers decreased rapidly

below a soil depth of 1 ft. Average depth of the longest root was 38 in.

Although blue grama root systems were similar in moderately grazed pastures and exclosures, their lateral spread was slightly less in moderately grazed pastures while maximum rooting depth was greater. The main roots in moderately grazed pastures also had slightly more rootlets per inch than in exclosures. Lateral spread was in the top 5-10 in. with a dense mat of roots being formed to a depth of about 6 in.

Roots from heavily grazed pastures were smaller, less branched, and shorter than those from moderately grazed or ungrazed areas. There were about 15-20 small 1/2-in. rootlets per inch on main roots. Most roots concentrated in the top 2-3 in. of soil.

Fringed sagebrush.—In ungrazed areas, fringed sagebrush has a semi-taproot arising from the many-branched plant crown. Lateral roots originate just below the soil surface and are often as large as the taproot, so that no definite taproot appears to exist. The roots are light brown, round, and taper toward the tip. Laterals usually grow horizontally 1-3 in. below the surface for several inches before descending vertically. Average maximum lateral spread of roots was 6 in. in ungrazed, 9 in. in moderately grazed, and 6 in. in heavily grazed pastures. Generally, the roots branched very little in the surface soil but had many branches at lower levels, often resembling grass roots. They attained depths of 38 in. in exclosures and moderately grazed pastures compared with only 26 in. in heavily grazed pastures. Roots from heavily used ranges had smaller diameters than those from ungrazed areas.

Pussytoes.—Pussytoes normally has a sparse, shallow, spreading root system. Roots are small, round, brown, taper toward the tip, and originate from the plant crown and from ground runners. Maximum lateral root spread of pussytoes was 5 in. in exclosures, 10 in. in moderately used pastures, and 6 in. in heavily used pastures. Average maximum depth of penetration was 14 in. in exclosures and moderately grazed pastures, and 19 in. in heavily grazed pastures.

Root patterns for the plant community

The overall difference in the plant community root patterns between grazing treatments was a change from dense, deep fibrous root systems under no grazing to shorter, less dense root systems as grazing use increased. The most obvious differences in root patterns were shallower rooting depth, smaller roots with less branching, and fewer roots at lower levels under the heavier grazing intensities. The differences were brought

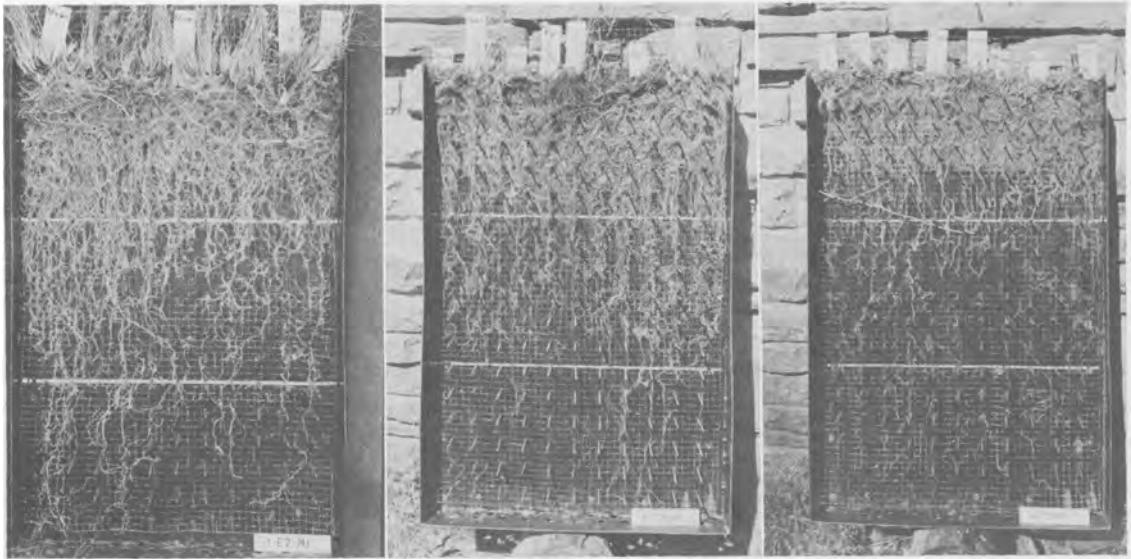


FIG. 6. Representative root systems taken from grassland areas that received (left) no grazing, (center) moderate grazing, and (right) heavy grazing. The horizontal white lines from top to bottom denote depths at 6 in., 1 ft, and 2 ft. The monoliths shown are to a depth of 3 ft. Species legend: Mumo = mountain muhly; Arfr = fringed sagebrush; Bogr = blue grama.

about by reduction in size and extent of the individual underground parts, and the change to species with less extensive root systems in moderately and heavily grazed pastures (Fig. 6).

The variations in root patterns correspond to compositional differences in aboveground vegetation. For example, mountain muhly and Arizona fescue predominated in ungrazed exclosures, where root systems were most extensive. Shorter-rooted species, such as blue grama, fringed sagebrush, and pussytoes, were progressively more important in moderately and heavily grazed pastures. This was paralleled by a corresponding decrease in size of the individual plants of the larger palatable species and consequently a smaller, less extensive community root pattern under heavy grazing.

DISCUSSION

Differences in root patterns between the three grazing intensities were created by differential grazing and plant responses. In the present study and others (Weaver 1950, Tomanek and Albertson 1957), the size and extent of the underground system in moderately and heavily grazed areas showed a decrease when compared with ungrazed areas. The decrease can be attributed to higher percentage utilization of palatable grasses than relatively unpalatable nongrass species as grazing increased. Increased grazing resulted in decreased depth of penetration, lateral spread and root weight of the grasses, while unpalatable species such as pussytoes were favored in moderately and heavily grazed pastures.

Root weights in the top foot of soil were in accord with Johnson's (1956) findings in an earlier study of the same pastures. The greater proportion of root weight in the top foot of soil under moderate and heavy use indicates that these intensities of grazing resulted in shorter root systems. This condition is due partially to the detrimental effect of grazing upon roots and partially to the shift toward shallower rooting species under heavy use. These findings are in agreement with Weaver (1950) who found that, as grazing intensity increased and tall grasses were replaced by short grasses and weeds, both depth of soil occupied by roots and the amount of root material decreased greatly. Thus, the effects of grazing may be compound in that, as root growth is limited by defoliation, it will be further limited by unavailability of nutrients and water because the root system occupies less soil space.

Ruby and Young (1953) found that grazing had a detrimental influence on the amount of roots in the soil below 12 in., but not on roots in the top 12 in. of soil. Thaine (1954) reported that the relative proportion of root material of Russian wildrye grass at varying depths was not influenced by clipping frequency. Cook et al. (1958) found that defoliation decreased root yields of crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.) more in the top 6 in. of soil than at greater depths. The differences in results reported by these investigators can possibly be explained by species, environmental, and treatment differences. In this study, as in that of Cook et al. (1958),

any grazing use caused a greater reduction in root weight in the top foot of soil than in other levels. The decline in root weight with grazing use was proportionately greater at deeper levels, however, when expressed on a percentage basis.

Stocking intensity had varied effects on the individual species. The size and extent of mountain muhly roots were inversely proportional to the intensity of grazing, which indicates that the amount of defoliation it received under moderate and heavy stocking proportionately reduced its root growth. Although Arizona fescue had a greater average maximum depth of rooting under moderate grazing than no grazing, it reacted in much the same manner as mountain muhly. On the other hand, the increase in extent of blue grama roots in moderately grazed areas with their subsequent decrease under heavy use implies that blue grama is favored by the defoliation it receives under moderate but not by that under heavy range use. It might logically be expected that a short-grass such as blue grama, which escapes close use by virtue of its low stature, would be favored by heavier use of the taller grasses. When grazing increased to the degree that blue grama was cropped excessively, however, its root system was reduced, indicating that it was released under moderate grazing because the dominant, more palatable plants were reduced. Weaver (1950) found similar effects of grazing pressure on blue grama. Tomanek and Albertson (1957) reported that the number of main and branch roots of blue grama was more detrimentally affected by heavy range use than was rooting depth. Observations on lateral spread and rooting depth in the present study indicated that this might possibly be true with Arizona fescue as well as with blue grama.

The root growth of fringed sagebrush and pussytoes was enhanced under moderate grazing, presumably because the vigor of the more palatable species was reduced. Fringed sagebrush roots, however, were smaller and less extensive in heavily grazed areas than in moderately grazed areas indicating a detrimental effect of continued overgrazing.

Although pussytoes apparently was not affected greatly by any intensity of range use, its roots were visibly less vigorous in the heavily grazed areas than the others. Although range deterioration is begun by the effects of grazing upon the plants, not all subsequent degeneration is due to the direct effect of defoliation.

SUMMARY

The purpose of this study was to examine the cumulative effects of two grazing intensities on the characteristics of individual plants and com-

munity root patterns on ponderosa pine-bunchgrass ranges. The species described specifically were mountain muhly, Arizona fescue, blue grama, fringed sagebrush, and Rocky Mountain pussytoes.

Root samples excavated from ranges grazed moderately and heavily for 17 years were compared with samples taken from ungrazed exclosures. The number of roots extending below the 2-ft soil depth level was similar in ungrazed and moderately grazed areas, but significantly less in heavily grazed pastures. Maximum root penetration was as deep under moderate grazing as in the ungrazed exclosures, but, with the exception of pussytoes, root extension was least under heavy grazing. Lateral root spread of the three grasses was proportionately less under moderate and heavy grazing, while lateral spread of fringed sagebrush and pussytoes was greatest under moderate grazing and approximately the same in ungrazed and heavily grazed areas.

Total root weight was reduced by moderate and heavy use. Grass root weight was significantly greater under no use than under moderate and heavy use, but nongrass root weight did not vary significantly. With the exception of nongrasses in ungrazed areas, 78% or more of the total root weight was found in the top 1-ft depth section. The proportion of total root weight found in the top foot of soil was greater in heavily grazed than in moderately grazed and ungrazed areas. Grazing apparently caused a greater reduction in root weight in the top 1-ft section than in other levels, but the decline in root weights with grazing was proportionately greater at deeper levels.

In general, the reductions in root systems were in proportion to the amount of use the individual species received under the given intensity of grazing. Root patterns under no grazing were dense, heavily branched, spreading, and deeply penetrating. Roots had progressively fewer branches and were sparser and shorter under moderate and heavy grazing.

LITERATURE CITED

- Albertson, F. W., A. Riegel, and J. L. Launchbaugh, Jr. 1953. Effects of different intensities of clipping on short grasses in west-central Kansas. *Ecology* 34: 1-20.
- Biswell, H. H., and J. E. Weaver. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. *Ecology* 14: 368-390.
- Cook, C. W., L. A. Stoddart, and F. E. Kinsinger. 1958. Responses of crested wheatgrass to various clipping treatments. *Ecol. Monographs* 28: 237-272.
- Crider, F. J. 1955. Root growth stoppage resulting from defoliation of grass. U. S. Dept. Agr. Tech. Bull. 1102, 23 p.
- Graber, L. F. 1931. Food reserves in relation to other

- factors limiting the growth of grasses. *Plant Physiol.* **6**: 43-71.
- Jacques, W. A. 1937. The effect of different rates of defoliation on the development of certain grasses. *New Zealand J. Sci. Technol.* **19**: 441-450.
- Johnson, W. M. 1953. Effect of grazing intensity upon vegetation and cattle gains on ponderosa pine-bunchgrass ranges of the Front Range of Colorado. U.S. Dept. Agr. Circ. 929, 36 p.
- . 1956. The effect of grazing intensity on plant composition, vigor, and growth of pine-bunchgrass ranges in central Colorado. *Ecology* **37**: 790-798.
- Parker, K. W., and A. W. Sampson. 1931. Growth and yield of certain Gramineae as influenced by reduction of photosynthetic tissue. *Hilgardia* **5**: 361-381.
- Ruby, E. S., and V. A. Young. 1953. The influence of intensity and frequency of clipping on the root system of brownseed paspalum (*Paspalum plicatulum* Michx.). *J. Range Mgmt.* **6**: 94-99.
- Thaine, R. 1954. The effect of clipping frequency on the productivity and root development of Russian wild-ryegrass in the field. *Canadian J. Agr. Sci.* **34**: 299-304 (abstract).
- Tomanek, G. W., and F. W. Albertson. 1957. Variation in cover, composition, production, and roots of vegetation on two prairies in western Kansas. *Ecol. Monographs* **27**: 267-281.
- Weaver, J. E. 1950. Effects of different intensities of grazing on depth and quantity of roots of grasses. *J. Range Mgmt.* **3**: 100-113.

EFFECTS OF SALINITY ON ALGAL DISTRIBUTION¹

LARS H. CARPELAN

*Division of Life Sciences
University of California, Riverside, Calif.*

INTRODUCTION

Gunter (1961) takes exception to a statement in Allee et al. (1949) to the effect that "salinity does not ordinarily function as a limiting factor for animal populations." Gunter is obviously correct in contending that the distributions of estuarine organisms are correlated with salinity.

Two matters seem to underlie the disagreement. One is the difference between estuaries, discussed by Gunter, and the more general problem, discussed by Allee et al. In estuaries there is a gradient of salinity which is absent from such bodies of water as inland mineral lakes and from coastal lagoons. Within the salinity gradient presented by an estuary, e.g., such as that reported by Alexander, Southgate, and Bassindale (1935) and reproduced in Harvey (1957), organisms with freedom of movement may, if other factors are equal, distribute according to their salinity optima. But in an isolated body of water, as in a lagoon cut off from the sea, there is no gradient. Unless the salinity happens to be optimal, the organisms present either live (survive) at sub- or super-optimal salinities, or, if these are intolerable, they perish. Distribution may thus be affected; abundance may or may not. (Although neither Gunter nor Allee et al. mention abundance, it is introduced here as a matter of concern, especially if we view this as an ecological problem in terms of Elton's definition of ecology as the study of dis-

tribution and abundance.) If food is plentiful, the size of population may equal that under optimal conditions of salinity but sub-optimal food availability. In other words, organisms are not restricted to optimal conditions, and any aquatic community will probably include species living at their optimal salinity, some below their optimum, and others above it.

This brings up the second matter of concern: the differences in tolerance among species. Allee et al. refer to this aspect of the problem when they argue that in environments with fluctuating salinity only euryhaline animals are present and in relatively constant salinities, the stenohaline species present are not subject to limitation by salinity changes.

Classed by tolerance, among both plants and animals there are stenohaline species, euryhaline species with various ranges of salt tolerance, and some species which are holeuryhaline. For the latter group salinity is not an operative factor (Mason and Langenheim 1957). Although salinity should limit distribution of euryhaline species to their limits of tolerance, the actual tolerance is seldom definitely known, and some species complicate matters by "adapting" to changes in salinity. For example, when trapped by formation of a coastal lagoon by closing of the estuary of an intermittent stream, organisms which might move to their salinity optima in the estuary can no longer do so because the salinity is the same throughout the lagoon. If the changes in salinity which then occur are slow, some of the individuals may become acclimated (or their progeny selected) and eventually live under conditions which would

¹ Supported by a grant (G-17860) from the National Science Foundation. Acknowledgment is made of the technical assistance of Carol Chaney Crosswhite, Markell W. Kohn, and Fred L. Zaebst, and of the taxonomic advice of Ruth Patrick, Paul L. Illg, and Boyd W. Walker.