

Effects of competition on spatial distribution of roots of blue grama

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Abstract

The spatial distribution of roots of the perennial grass blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths] was evaluated under 2 competitive conditions. The radioisotope ^{14}C was used to label roots of blue grama plants growing with and without neighboring plants of the same lifeform. The majority of labeled blue grama roots (>75%) were found within 5 cm of the plant and within 10 cm of the soil surface. Labeled roots extended at least 30 cm from the edge of the plant and to depths of at least 90 cm. Root system morphology was insensitive to changes in competitive conditions. Based on our estimates of the depth and breadth of the root system of an average blue grama plant, roots associated with at least 4 other blue grama plants of average size and separated by average distances of 10 cm might occur within the volume of soil associated with roots of this plant. The distribution of total root biomass was not representative of the distribution of labeled roots, even when neighboring grasses were removed.

Key Words: root distribution, intralifeform competition, shortgrass steppe, ^{14}C , radioisotope labeling, plant community structure

In the shortgrass steppe and other semiarid grasslands, soil water is the most frequent control on plant growth and community structure (Noy-Meir 1973, Lauenroth et al. 1978, Parton et al. 1981). Shortgrass steppe plant communities of the central and southern Great Plains of the United States are dominated by the perennial grass, blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths], which accounts for 75–90% of aboveground net primary production on most sites (Dodd and Lauenroth 1979). Because of the overwhelming dominance by blue grama, the strongest competitive interactions for belowground resources in these grasslands is most likely between individual blue grama plants rather than between plants of different species or lifeforms (e.g., Cable 1969, Parrish and Bazzaz 1976).

Spatial distributions of roots of grassland species have been evaluated in several ways, including the use of soil pits (e.g., Weaver 1919, 1958) and radioactive tracers, such as ^{14}C and ^{32}P (e.g., Neilson 1964, Reynolds and Fraley 1989). Several studies have been conducted in shortgrass communities to evaluate the distribution of total (Bartos and Sims 1974, Leatham and Milchunas 1985, Liang et al. 1989) and labeled root biomass (Singh and Coleman 1974, Lee 1990). However, the spatial distribution of total and labeled roots of individual blue grama plants, effects of neighboring grasses on the distribution, and the relationship between the distribution of total and labeled root biomass have not been evaluated. The objectives of this study were to evaluate: (1) the spatial distribution of roots of blue grama plants; (2) the effects of intra-lifeform competition on the root distribution; (3) the overlap in root systems among neighboring blue grama plants; and (4)

the relationship between the distribution of labeled roots of a blue grama plant and the distribution of total root biomass.

Methods

Study was conducted at the Central Plains Experimental Range (CPER). The CPER is located in northcentral Colorado, USA, approximately 60 km northeast of Fort Collins (40° 49' N, 107° 47' W). Mean annual precipitation over the past 45 years was 311 mm (SD = 79 mm) and mean monthly temperatures ranged from -5° C in January to 22° C in July. Moderate grazing by cattle occurs throughout the area. Relative basal cover of all plants at most sites ranges from 25–40%, of which 85–90% is accounted for by blue grama (Milchunas et al. 1989). A number of other perennial grasses, succulents, shrubs, and forbs account for the remainder.

In 1982, 10 blue grama plants were randomly selected within a 0.5-ha temporary cattle enclosure. Five of these were randomly selected as controls. Each of the 5 remaining plants occupied the center of a 1-m radius circle from which all other grass individuals were removed by clipping below the soil surface (grass removals). Removal of grasses continued on a monthly basis during the 1982–1985 growing seasons until the blue grama plants were labeled with ^{14}C as $^{14}\text{CO}_2$ on 25 July 1985.

The labeling procedure was adapted to field conditions from Milchunas et al. (1985). Clear plastic tents supported by aluminum tubing were placed over each of the 10 blue grama plants. The tents were secured at the base with soil to prevent $^{14}\text{CO}_2$ leakage during the labeling period. After an initial drawdown of CO_2 , approximately 3.7×10^5 Bq (10 microCi) ^{14}C per gram of aboveground plant tissue were released into the tent. Biomass of each plant was estimated using the aboveground surface area of the plant (m^2) and the average biomass of blue grama on an area basis (g/m^2). The time necessary to reach the CO_2 compensation point was estimated by monitoring $^{14}\text{CO}_2$ in the tents with a thinend-window Geiger-Mueller meter. When the ^{14}C level no longer declined, unlabeled CO_2 was released in the tent. Three drawdowns of CO_2 after the release of the $^{14}\text{CO}_2$ resulted in an uptake efficiency of approximately 95%. The tents were manually shaken to promote airflow and the temperature inside the tents was monitored throughout the 2-hour labeling period.

Sampling did not begin until at least 4 weeks after labeling to allow the incorporation of labile ^{14}C into structural compounds. Paired (5-cm diameter, 90-cm deep) samples were collected along three 30-cm lines radiating (0°, 90°, and 180°) from the center of each plant. Samples were collected at 5, 15, and 30 cm from the edge of each plant. Each pair was combined to form 1 sample with only a single pair being extracted from the center of each plant (total n/plant = 10). Each core was separated into depth increments of 0–10, 10–25, 25–50, and 50–90 cm. The remaining half of each quadrat was utilized in an excavation study of blue grama roots (Lee 1990).

Roots (live and dead) were separated from the soil with a hydropneumatic elutriation system that uses air and water pressure to deposit roots on a fine mesh screen (Smucker et al. 1982). Root material was dried at 100° C, weighed, and ground through a micro-Wiley mill to pass a 40-mesh screen. Plant material was combusted in a Packard Model 306 tri-carb sample oxidizer using

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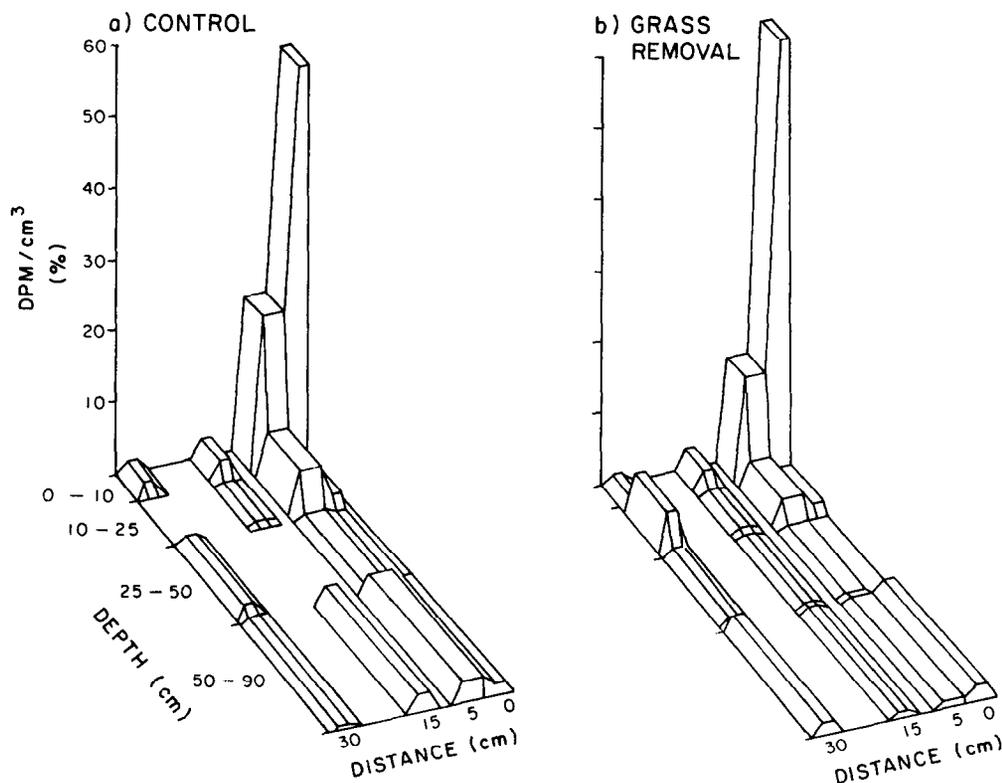


Fig. 1. Location of labeled roots (% of total DPM/cm³) by depth and distance for blue grama plants (a) without (control) and (b) with neighboring grasses removed (grass removal). No significant differences between treatments. Within each treatment, percentages of labeled roots found beneath and at 5 cm distance are significantly different from each other and from the remaining depths and distances ($P < 0.05$). Remaining depths and distances are not significantly different from each other.

a Carbosorb CO₂ trap and Permaflour cocktail. ¹⁴C activity was determined by liquid scintillation counting. Data are reported on an ash-free, quench, and background-corrected basis.

Disintegrations per minute on a volume basis (DPM/cm³) for each depth and distance from the edge of a plant were calculated and summed to obtain a total DPM for the plant. Percentage of the total DPM at each depth and distance was used to estimate the location of labeled roots for plants with and without neighboring grass plants.

Analysis of variance was used to evaluate effects of the removal of plants and location of roots by depth and distance from the shoot on labeled roots and biomass of roots in a 2×4×4 factorial design. Tukey's Q values were used to compute least significant ranges (LSR) and to evaluate significantly different means at the $P < 0.05$ level (Sokol and Rohlf 1981).

Overlap in root systems of neighboring blue grama plants was calculated using the location of the labeled roots and an estimated average distance between plants (10 cm; based on the size distribution and basal cover of blue grama plants from Coffin and Lauenroth [1988]). Calculation of the proportion of roots attributed to each plant at each distance location (0, 5, and 10 cm) was based on the calculated overlap in the distribution of labeled roots for 2 adjacent plants. Values for 10 cm were estimated by interpolating between the 5 and 15 cm distances. Spatial heterogeneity of root densities at a particular depth in the soil, as well as among depths, was evaluated using the total calculated amount of roots at each location between 2 blue grama plants.

Results and Discussion

Spatial Distribution of Blue Grama Roots

Labeled roots from individual blue grama plants, with or without neighboring grass plants, extended at least 30 cm from the edge

of the plant and to a depth of at least 90 cm (Fig. 1). A large proportion of labeled roots from plants with (>77%) and plants without neighboring grasses (>75%) was found directly beneath and at the edge (5 cm distance) of the target blue grama plant in the upper 10 cm of the soil. Percentages of labeled roots found beneath and at 5-cm distance from the plant were significantly different from each other and from the remaining depths and distances. The remaining depths and distances were not significantly different from each other.

The dominance and persistence of blue grama in this region is likely related to the functional aspects of its root distribution relative to the distribution of water in the soil profile (Lauenroth et al. 1978). Most precipitation events (>80%) in the shortgrass region are small (≤ 5 mm) (Sala and Lauenroth 1982) and they wet only the upper soil layers where the majority of blue grama roots are located. As such, blue grama can respond rapidly to small amounts of rainfall (Sala and Lauenroth 1982, Lauenroth et al. 1987). Likewise, this pattern of distribution of roots suggests blue grama has the structural capacity to access water stored at relatively deep depths in the soil profile (90 cm) during intervals between small rainfall events.

Effects of Competition on Blue Grama Root Distribution

Distributions of labeled roots of plants with and without neighboring grasses were not significantly different (Fig. 1). The absence of any measured effect of neighboring grass plants on the labeled rooting pattern of blue grama suggests that a blue grama plant has only a limited ability to exploit resources beyond the edge of its canopy (>10 cm), regardless of resource availability. Factors related to soil type, including bulk density, texture, and impediments, might also be contributing factors affecting root depth and spatial extension of blue grama plants (Weaver and Darland 1949, Fox et al. 1953). Our results suggest, however, that full-size blue

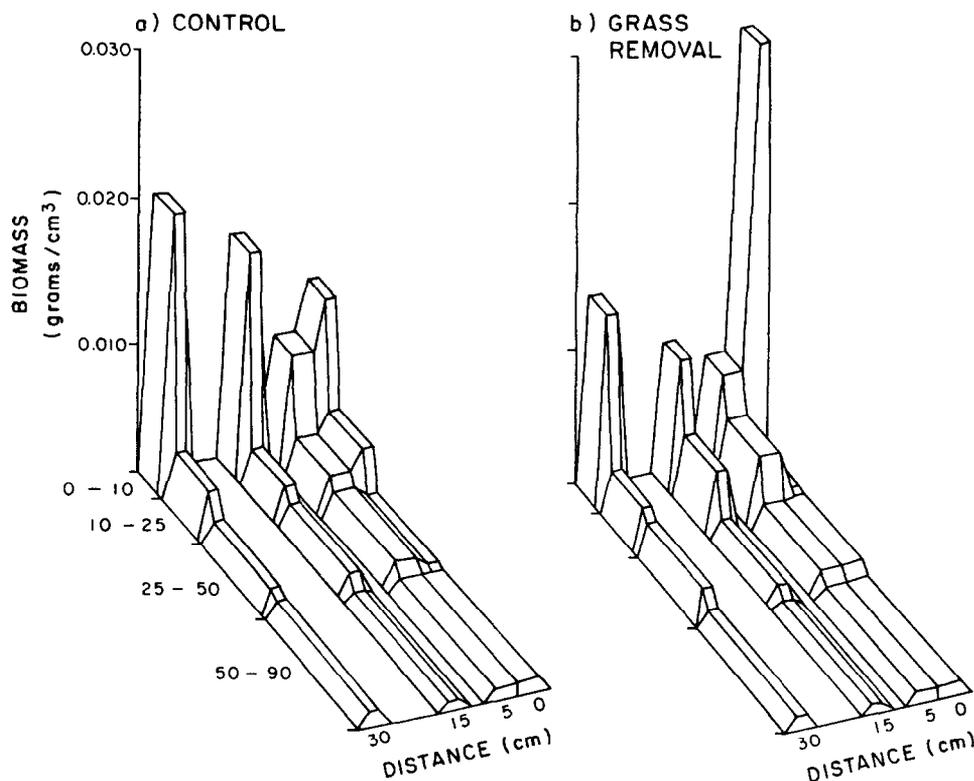


Fig. 2. Location of total root biomass (g/cm^3) by depth and distance for blue grama plants (a) without (control) and (b) with neighboring grasses removed (grass removal). No significant differences between treatments, depths or distances.

grama plants growing on a particular soil type would be expected to have similar root distributions.

Overlap in Blue Grama Root Systems

The relatively small estimated average distance between neighboring blue grama plants, as compared to the rather broad spatial distribution of their roots, resulted in a large degree of calculated overlap in root systems between neighboring plants. The analysis showed roots of both plants occurred at each of 12 depth and distance locations from the target plant (Table 1a). The greatest potential for intraspecific competitive interactions, based on the same percentage of roots of both plants at a particular location, occurred beneath the plants for depths from 10–50 cm, and by definition, for all depths in the space between plants (Table 1a). Most roots beneath a plant and within 10 cm of the soil surface (87%) belonged to that plant rather than to a neighboring plant.

Table 1. Calculated overlap of labeled roots for 2 blue grama plants separated by 10 cm.^{1,2}

(a) Percentage contribution of targeted blue grama plant roots to total roots present at various depths and distances from targeted plant.

Depth (cm)	Distance (cm)		
	0	5	10
0–10	87	50	13
10–25	50	50	50
25–50	50	50	50
50–90	36	50	64

The root system of a blue grama plant may interact with roots of a number of other blue grama plants. Based on our estimates of the depth and breadth of the root system, the total volume occupied by roots of an average full-size blue grama plant with a basal cover of

320 cm^2 is 0.45 m^3 . Roots of at least 4 other blue grama plants of average size and separated by average distances of 10 cm may occur within the volume of soil associated with roots of this plant.

Spatial heterogeneity of root densities between 2 blue grama plants, based on the total calculated amount of roots at each location, indicated areas of relatively low root biomass at the soil surface between plants, and beneath the plants at other depths (Table 1b). Microsite variability in root densities of blue grama

Table 1. (continued)

(b) Total amount of labeled roots (sum of % activity at each location) for 2 plants.

Depth (cm)	Distance (cm)		
	0	5	10
0–10	64.4	43.6	64.4
10–25	3.5	12.4	3.5
25–50	0.3	1.6	0.3
50–90	4.1	5.7	4.1

¹Distribution of roots for each plant is from Fig. 1a.

²Values for 10 cm were estimated using the mean of percentages from the 5 and 15 cm distances.

may be a result of differences in resource availability, morphologic constraints on rooting patterns, or a combination of factors. Additional experimental studies are necessary to distinguish among these possibilities. Spatial heterogeneity in root biomass for grass species has also been found in a Patagonian steppe community (Soriano et al. 1987).

Relationship Between Labeled and Total Root Biomass Distributions

The majority of total sampled root biomass (labeled and unlabeled) for plants with and without neighboring grass plants occurred in the upper 10 cm of the soil profile (>70%) whereas the

upper 25 cm contained greater than 87% of the biomass (Fig. 2). The location of the majority of root biomass in the upper soil layers is consistent with previous estimates for shortgrass plant communities (Bartos and Sims 1974, Singh and Coleman 1974, Leetham and Milchunas 1985, Liang et al. 1989). The distribution of total root biomass was not representative of the distribution of labeled roots, even when neighboring grasses were removed. The distribution of labeled roots and total root biomass were not similar for plants with (Figs. 1a, 2a) or without neighboring plants (Figs. 1b, 2b). This lack of correspondence between the 2 distributions was the result of important contributions to biomass by neighboring plants for control plants, while large quantities of dead roots, presumably from the neighboring grass plants that had been killed, were found during an excavation of the plots where removals had occurred (Lee 1990).

Conclusions

The dominance of blue grama in shortgrass steppe plant communities is likely related to the vertical and horizontal distribution of its root system. The limited ability of blue grama root distributions to respond to the presence or absence of neighboring plants might be important for the persistence of other species and maintenance of species diversity in these communities, especially after disturbances. The large potential for competitive interactions between neighboring blue grama plants is also likely to be an important factor for plant community structure. The poor relationship between the distribution of labeled roots and distribution of total root biomass suggests caution should be exercised in sampling root systems of individual plants.

Literature Cited

- Bartos, D.L., and P.L. Sims. 1974.** Root dynamics of a shortgrass ecosystem. *J. Range Manage.* 27:33-36.
- Cable, D.R. 1969.** Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction. *Ecology* 50:27-38.
- Coffin, D.P., and W.K. Lauenroth. 1988.** The effects of disturbance size and frequency on a shortgrass plant community. *Ecology* 69:1609-1617.
- Dodd, J.L., and W.K. Lauenroth. 1979.** Analysis of the response of a grassland ecosystem to stress, p. 43-58. *In:* N.R. French (Ed.). *Perspectives in grassland ecology*. Ecological Studies Vol. 32. Springer-Verlag, New York.
- Fox, R.L., J.E. Weaver, and R.C. Lipps. 1953.** Influence of certain soil-profile characteristics upon the distribution of roots of grasses. *Agron. J.* 45:583-589.
- Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978.** The effects of water-and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia (Berl.)* 36:211-222.
- Lauenroth, W.K., O.E. Sala, D.G. Milchunas, and R.W. Lathrop. 1987.** Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Function. Ecol.* 1:117-124.
- Lee, C.A. 1990.** The spatial distribution of root systems for three plant life-forms in the shortgrass steppe. M.S. Thesis. Colorado State Univ., Fort Collins.
- Leetham, J.W., and D.G. Milchunas. 1985.** The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass, and grazing by cattle. *Pedobiologia* 28:311-325.
- Liang, Y.M., D.L. Hazlett, and W.K. Lauenroth. 1989.** Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe. *Oecologia (Berl.)* 80:148-153.
- Milchunas, D.G., W.K. Lauenroth, P.C. Chapman, and M.K. Kazempour. 1989.** Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80:11-23.
- Milchunas, D.G., W.K. Lauenroth, J.S. Singh, C.V. Cole, and H.H. Hunt. 1985.** Root turnover and production by ^{14}C dilution: Implications of carbon partitioning in plants. *Plant and Soil* 88:353-365.
- Neilson, J.A., Jr. 1964.** Autoradiography for studying individual root systems in mixed herbaceous stands. *Ecology* 45:644-646.
- Noy-Meir, I. 1973.** Desert ecosystems: Environment and producers. *Annu. Rev. Ecol. Syst.* 4:25-52.
- Parrish, J.A.D., and F.A. Bazzaz. 1976.** Underground niche separation in successional plants. *Ecology* 57:1281-1288.
- Parton, W.J., W.K. Lauenroth, and F.M. Smith. 1981.** Water loss from a shortgrass steppe. *Agr. Meteorol.* 24:97-109.
- Reynolds, T.D., and L. Fraley, Jr. 1989.** Root profiles of some native and exotic plant species in southeastern Idaho. *Environ. Exp. Bot.* 29:241-248.
- Sala, O.E., and W.K. Lauenroth. 1982.** Small rainfall events: An ecological role in semiarid regions. *Oecologia (Berl.)* 53:301-304.
- Singh, J.S., and D.C. Coleman. 1974.** Distribution of photo-assimilated ^{14}C in the root system of a shortgrass prairie. *J. Ecol.* 62:359-365.
- Smucker, A.J.M., S.L. McBurney, and A.K. Srivastava. 1982.** Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. *Agron. J.* 74:500-503.
- Sokal, R.R., and F.J. Rohlf. 1981.** *Biometry*. Second Ed., Freeman, New York.
- Soriano, A., R.A. Golluscio, and E. Satorre. 1987.** Spatial heterogeneity of the root system of grasses in the Patagonian arid steppe. *Bull. Torrey Bot. Club* 114:103-108.
- Weaver, J.E. 1919.** The ecological relations of roots. *Cargenie Inst. Wash. Pub.* 286.
- Weaver, J.E. 1958.** Summary and interpretation of underground development in natural grassland communities. *Ecol. Monogr.* 28:55-78.
- Weaver, J.E., and R.W. Darland. 1949.** Soil-root relationships of certain native grasses in various soil types. *Ecol. Monogr.* 19:303-338.