Competition between cheatgrass and two native species after fire: Implications from observations and measurements of root distribution

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Abstract

During 1987 and 1988, a study was conducted in northern Nevada to examine root growth of cheatgrass (*Bromus tectorum* L.) and 2 native species, needle-and-thread grass (*Stipa comata* Trin. & Rupr.) and rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.), after fire. Profile wall maps were used to determine the distribution of roots in the soil profile for the 2 native species. Root morphology differed between the 2 species: needle-and-thread grass had a flabelliform root system, whereas rabbitbrush had a main tap root with 2–4 major lateral roots. Although total root biomass differed between the species, more than half the root biomass was in the top 0.2 m of soil for both needle-and-thread grass and rabbitbrush. Measurements of root length density were used to evaluate the interaction between root systems of cheatgrass and the native species. Root production of plots with only the native species was not significantly different from that of plots with both the native species and cheatgrass for the first 2 years after fire. Furthermore, root production of plots in a recently burned area was also not significantly different from that in an area burned 12 years prior to our study. Thus, root systems of these species rapidly occupied the belowground space and competed for soil resources after fire, and the presence of cheatgrass partially reduced the root systems of the native species.

Key Words: *Chrysothamnus viscidiflorus,* rabbitbrush, *Stipa comata,* needle-and-thread grass, root length density, root biomass

Roots are the primary structures that plants have to utilize belowground resources, but very little is known about how root growth responds after fires. Fire affects the availability of soil resources (Britton and Ralphs 1979). Burning converts plant biomass into ash, which releases nutrients (Raison 1979, Wright and Bailey 1982). Soil water is influenced by fire (Daubenmire 1968, Wright and Bailey 1982), increasing or decreasing the amount of water present in the soil (Anderson et al. 1970). Soil resources are also freed by the loss of fire-intolerant plants. Root growth and density are coupled to uptake of nutrients (Silberbush and Barber 1985, Caldwell and Richards 1986) and water (Caldwell 1976, Lascano and van Bavel 1984). Thus, root growth after fire may influence how plants exploit newly available nutrients and acquire sufficient moisture for enhanced shoot growth (Raison 1979, Hadley and Kieckhefer 1963).

Cheatgrass (*Bromus tectorum* L.) is well adapted to frequent fire and often dominates plant communities after fire (Young et al. 1969). The success of cheatgrass after fire has often been attributed to its capability to rapidly occupy the open spaces created by the removal of fire-intolerant plants (Stewart and Hull 1949, Klemmedson and Smith 1964, Young et al. 1969, Young and Evans 1973, Thill et al. 1984). Recently, we found that cheatgrass also successfully competes for soil water with native species that survive the fire (Melgoza et al. 1990). This capability of cheatgrass to successfully compete with its neighbors may be related to differences in their capacities to extend root systems after fire. However, how roots of cheatgrass and established adult perennials compete for and exploit the soil resources available after fire in sagebrush (*Artemisia tridentata* Nutt.) ecosystems is unknown.

This study describes the distribution of roots for 2 native species: needle-and-thread grass (*Stipa comata* Trin. & Rupr.) and rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.). It also investigates the spatial distribution of roots after fire for these 2 species and how competition with cheatgrass affects rooting characteristics. Finally, because results from a 2-year study after fire may not accurately predict changes that occur during extended periods of time after fire, we compared root production of a recently burned area with that from an area that burned 12 years prior to our study.

Methods

Study Area

The study plots were located in 2 adjacent areas: a 1-ha area that was naturally burned during late-summer 1986 and a 0.7-ha area that had not burned for at least 12 years. The recently burned study area probably resulted from an isolated lightning strike that was quickly extinguished because of accompanying rain and low fuel load. The second study area served as a "long-term reference" to compare rooting characteristics after an extended post-fire period of time with those during the first 2 years after a fire. Both areas were fenced to exclude grazing.

Soil characteristics of the recently burned and long-term reference areas were similar. We dug 2 soil pits, one in each study area. Soils were classified as coarse-loamy, mixed, mesic, Xerollic Haplargids. Soils were very deep (depth to bedrock exceeded 2 m) and well drained with 15–25% surficial coarse fragments. The study areas were on a remnant summit of a fan piedmont, and parent material was alluvium from nearby granitic mountains. Average slope was 2% with a west-southwest aspect. Soils also have been mapped to the same unit, which belongs to the Bedell series (Baumer 1983).

Vegetative characteristics of the adjacent study areas were also similar. Both areas were in the middle of a sagebrush-bunchgrass community. Sagebrush, rabbitbrush, needle-and-thread, horsebrush (*Tetradymia canescens* DC.), squirreltail (*Sitanion hystrix* (Nutt.) J.G. Smith), and the introduced species cheatgrass were the dominant species in the community. Average precipitation was estimated to be 250 mm (Evans and Young 1977). Measurements were taken during 1987 and 1988, which had 95% and 50% of estimated normal precipitation, respectively. The study areas (39°51'N, 119°48'W) were 35 km north of Reno, Nevada at 1,570 m elevation.

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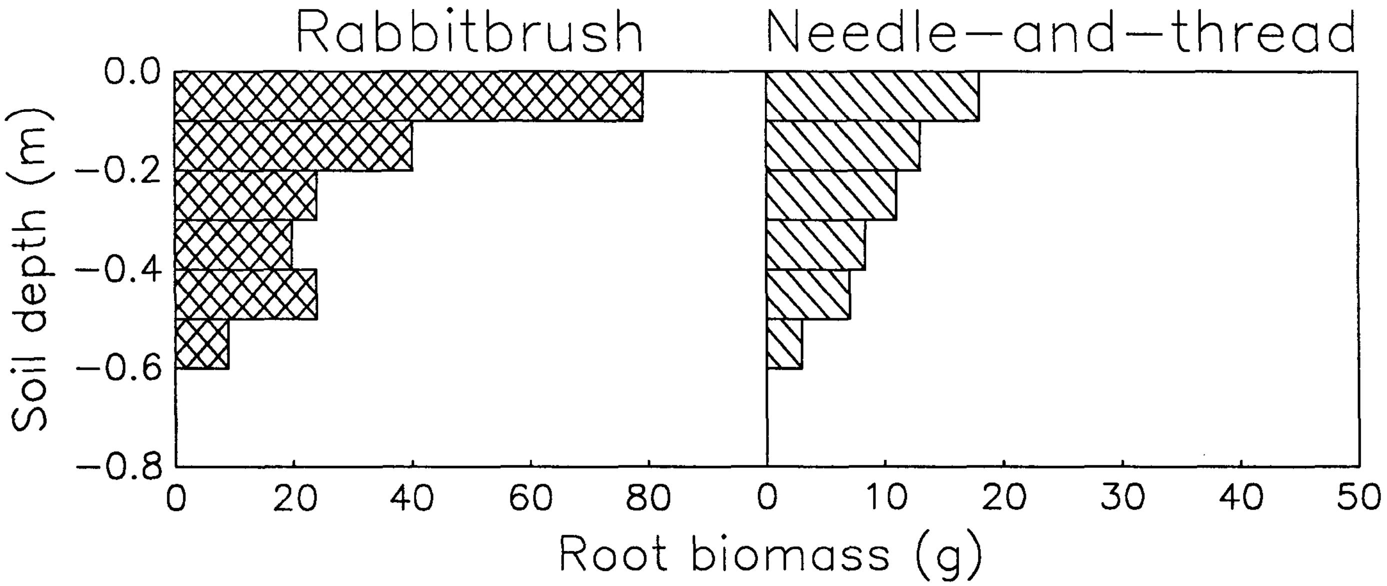

Fig. 1. Root biomass distribution for 2 rabbitbrush plants (left frame) and 2 needle-and-thread grass plants (right frame). Root systems were excavated by hand from a trench dug 0.2 m away from each individual. Note the different x-axis scales for the 2 species.

Target Species

Two native species that are relatively resistent to fires in late summer, rabbitbrush, and needle-and-thread grass (Young 1983), were selected to determine the effects of fire and cheatgrass competition on root growth and density. Rabbitbrush is a perennial, undesirable shrub and needle-and-thread grass is a perennial, desirable bunchgrass. At the beginning of the study, we selected plants that were similar in size based upon measurements of basal area. Sixteen target individuals of each species in the recently burned area were selected with stratified random technique to assure adequate size and spatial interspersion (Hurlbert 1984). Eight target individuals of each species in the long-term reference area were selected using the same technique. These target individuals were the same ones used for soil water measurements in Melgoza et al. (1990).

In order to determine the short-term effects of cheatgrass competition on root growth after fire, we established plots with and without cheatgrass. All plants within a 1.0-m radius around target individuals in the recently burned area (plots without cheatgrass) were removed with a hoe during fall 1986. Many of the plants removed from the burned area appeared to be dead, but were removed to insure a uniform competitive environment among plots. During the next 2 years, cheatgrass as well as seedlings of other plants were removed as needed from the plots. Plots of target individuals with cheatgrass were established in an analogous manner: all plants except cheatgrass were removed during fall 1986 and as needed during the next 2 years.

The long-term reference area provided information on what may occur at 12 years after fire. Vegetation in the long-term reference area was not altered. Thus, these plots served as an extended time reference for rooting characteristics in a competitive environment many years after fire rather than as a strict experimental control for the treatments in the recently burned area.

Root Observations

Direct root observations of the 2 native species were made during 1987. Trenches about 2-m deep and 5-m long were dug about 0.2 m from 2 individuals of each target species to provide access for root excavation. The soil on the trench wall was carefully removed by hand to uncover the root systems of individual rabbitbrush and needle-and-thread plants. Although fine roots were lost in the process, profile wall maps of the root systems provided information about root form and underground distribution of biomass of larger roots. Root form and distribution was recorded to 0.6-m soil depth, and root biomass at 0.1-m depth increments was clipped, oven-dried, and weighed.

Root Growth and Density

Root length density was determined by destructive sampling. Soil cores were taken with a 35-mm diameter auger at 2 locations: the edge of the target plant canopy and 0.5 m away from the edge. We made 2 assumptions when we selected these locations. First, the volume of soil below the canopy of the plant represents soil that is probably dominated by the plant (Caldwell and Richards 1986, Manning and Barbour 1988). Second, the volume of soil at 0.5-m distance represents a soil resource that was probably dominated by another plant but became available after the removal of that other plant by fire. These assumptions were verified by our profile wall maps.

Soil cores were taken from each plot at the end of each growing season (July 1987 and August 1988). Root cores were taken at the following depth increments: 0.0–0.3, 0.3–0.5, 0.5–0.7, 0.7–0.9, 0.9–1.1, and 1.1–1.4 m depth. Samples were washed free from soils using a hydropneumatic root washer (Gillison's Variety Fabrication Inc., Benzonia, Michigan) (Smucker et al. 1982). Organic material was manually removed from samples. Live and dead roots were differentiated by a staining technique (Ward et al. 1978). Root length was measured with a Comair root length scanner (Commonwealth Aircraft Corporation Limited, Melbourne, Australia).

Although we could differentiate between live and dead roots, we could not reliably differentiate among species. Thus, we assumed that roots were from the plants that were present in the 1-m diameter plots. For example, live roots in soil cores from plots without cheatgrass in the recently burned area were undoubtedly from the target individual of that plot. For soil cores from plots with cheatgrass, roots were from both the target individual and cheatgrass.

Statistical Analyses

Data were analyzed using split-plot types of analysis of variance (ANOVA). We had 2 dependent variables: root length density at each depth increment and root length density for the 1.4-m deep soil profile. Whole-plot treatments had 3 levels: recently burned area without cheatgrass, recently burned area with cheatgrass,

Table 1. Split-split-split plot analysis of variance (ANOVA) for root density data from individual depth increments.

Source[1]	d.f.[2]	P values Chvi plots[3]	 Stco plots[4]
Treatment	2	0.355	0.478
Treatment*Plot (error)	21		
Year	1	0.000	0.001
Treatment*Year	2	0.629	0.656
Treatment*Year*Plot (error)	21		
Location	1	0.024	0.454
Treatment*Location	2	0.777	0.655
Year*Location	1	0.001	0.756
Treatment*Year*Location	2	0.569	0.778
Treatment*Year*Location*Plot (error)	42		
Depth	5	0.000	0.000
Treatment*Depth	10	0.800	0.069
Year*Depth	5	0.000	0.032
Location*Depth	5	0.001	0.059
Treatment*Year*Depth	10	0.931	0.061
Treatment*Location*Depth	10	0.966	0.590
Year*Location*Depth	5	0.112	0.750
Treatment*Year*Location*Depth	10	0.398	0.411
Treatment*Year*Location* Depth*Plot (error)	420		
Total	575		

[1] Sources of variation are: Treatment = whole-plot treatments of presence/absence of cheatgrass in recently-burned area and long-term reference; Year = 1987/1988; Location = edge of canopy/0.5 m from edge; Depth = soil depth increments of 0.0–0.3, 0.3–0.5, 0.5–0.7, 0.7–0.9, 0.9–1.1, 1.1–1.4; Plot = experimental unit.

[2] Degrees of freedom

[3] ANOVA from plots with rabbitbrush as the target individual

[4] ANOVA from plots with needle-and-thread grass as the target individual.

and long-term reference area. Year (2 levels) and location (i.e., lateral distance from the target individual, 2 levels) were subplot factors for both dependent variables, and depth (6 levels) was an additional subplot factor for root length density at each depth increment. Our experimental unit, the individual plots of target plants, had 8 replications. Each species was analyzed separately. Because only the cheatgrass removal, whole-plot treatment factor was randomly applied to experimental units and because only 1 recently burned area was sampled, the assumption that whole-plot treatments were applied randomly to all experimental units (Winer 1971, Steel and Torrie 1980) was compromised. Nonetheless, a split-plot ANOVA was a reasonable method for statistical analysis, especially because data were taken on an individual plant basis, which were a stratified-random sample of the available population. However, extrapolation of our results to other burned areas cannot be justified on a statistical basis.

The level of significance was $P<0.05$. First, we determined which interaction terms from the ANOVA were significant, then grouped means for these significant interaction terms using L.S.D. techniques (Steel and Torrie 1980:381). Next, we determined which whole-plot or subplot factors were significant, and again grouped means using L.S.D. mean comparisons. Although the L.S.D. test is less conservative than other mean comparisons, we agreed with Snedecor and Cochran (1967:275): "For routine purposes, thoughtful use of either the L.S.D. or the Newman-Keuls method should be satisfactory."

Results

Root Observations

The root system of rabbitbrush was characterized by a main tap root at least 0.6 m deep, with some major, secondary roots extended laterally over 0.6 m and many fine roots. Needle-and-thread grass had a flabelliform root system, about 0.5-m wide. Excavations for root observations were stopped when the silica-cemented horizon was reached (at about 0.6 m depth) because it became very difficult to track roots. Below 0.6 m, roots were few and very fragile. More than 50% of the total root biomass for both species was distributed in the upper 0.2 m of soil depth (Fig. 1).

Root Length Density

Three interaction terms and 3 subplot factors were significant from the split-split-split plot ANOVA of root length density data for individual depth increments from plots with rabbitbrush plants as the target individual (Table 1). From the mean comparisons for the Location*Depth interaction term, root length densities near the edge of the target plant's canopy were significantly greater than those 0.5 m away from the edge only for the 0.0–0.3 m depth increments (Table 2a). Root length densities for the 5 depth increments below 0.3 m were not significantly different between locations. The Year*Depth interaction term was also significant: individual depth increments overlapped to a greater extent in 1987 than in 1988 (Table 2b). For example, the 0.3–0.5 depth increment was significantly greater than the 0.5–0.7 increment in 1988, but not in 1987. Mean comparisons for the Year*Location interaction term showed that locations were significantly different in 1988, but not in 1987 (Table 2c). Thus, 2 of the significant subplot factors, Depth and Location (Tables 1, 2d, 2e) are moderately confounded by the significant interaction terms. However, the significant Year subplot factor (Table 2f) is more consistent: root length density in 1988 is almost always greater than that in 1987.

Table 2. Mean comparisons for root length density (cm cm^{-3}) from individual depth increments for plots with rabbitbrush as the target individual.

------ (a) Locations by depth (Location*Depth interaction term) ------

Depth increment	Canopy edge	0.5 m from edge
0.0–0.3 m	15.0a[1]	8.2b
0.3–0.5 m	8.2a	6.4a
0.5–0.7 m	5.1a	3.8a
0.7–0.9 m	5.4a	4.6a
0.9–1.1 m	4.4a	3.6a
1.1–1.4 m	3.3a	3.5a

---------- (b) Depths by year (Year * Depth interaction term) ----------

Year	Depth increment 0.0–0.3 m	 0.3–0.5 m	 0.5–0.7 m	 0.7–0.9 m	 0.9–1.1 m	 1.1–1.4 m
1987	6.0b	3.2a	2.2a	3.1a	1.7a	2.8a
1988	17.2d	11.3c	6.6b	6.8b	6.2ab	4.0a

------- (c) Locations by year (Year*Location interaction term) -------

Year	Canopy edge	0.5 m from edge
1987	2.7a	3.7a
1988	11.0b	3.4a

---------------- (d) Depth increment subplot factor ----------------

0.0–0.3 m	0.3–0.5 m	0.5–0.7 m	0.7–0.9 m	0.9–1.1 m	1.1–1.4 m
11.6c	7.3b	5.0a	4.4a	4.0a	3.4a

---------------- (e) Location subplot factor ----------------

Canopy edge	0.5 m from edge
6.9b	5.0a

---------------------- (f) Year subplot factor ----------------------

1987	1988
3.2a	8.7b

[1] Mean comparisons were made with an L.S.D. test; means within a row that have the same letter did not differ significantly ($P>0.05$).

The ANOVA for root length density data from individual depth increments for plots with needle-and-thread grass at target individuals had fewer significant terms than that for rabbitbrush plots.

Table 3. Mean comparisons for root length density ($cm\ cm^{-3}$) from individual depth increments for plants with needle-and-thread grass as the target individual.

(a) Depths by year (Year*Depth interaction term)

Year	0.0–0.3 m	0.3–0.5 m	0.5–0.7 m	0.7–0.9 m	0.9–1.1 m	1.1–1.4 m
	Depth increment					
1987	7.1c[1]	3.5b	3.2b	2.2ab	1.7ab	0.6a
1988	13.8d	10.6c	6.7b	6.1ab	8.0b	4.4a

(b) Depth increment subplot factor

0.0–0.3 m	0.3–0.5 m	0.5–0.7 m	0.7–0.9 m	0.9–1.1 m	1.1–1.4 m
10.5d	7.0c	4.9b	4.9b	4.1b	2.5a

(c) Year subplot factor

1987	1988
3.0a	8.3b

[1] Mean comparisons were made with an L.S.D. test; means within a row that have the same letter did not differ significantly ($P>0.05$).

Only 1 interaction term and 2 subplot factors were significant (Table 1). As with rabbitbrush plots, the significant Year*Depth interaction term (Table 3a) confounded the significant Depth subplot factor (Table 3b): the grouping of means for individual depth increments differed between years. Root length density in 1988 was significantly greater than that in 1987 (Table 3c).

The most important aspect of these ANOVA's was the lack of significance for any term involving the whole-plot Treatment factor (Table 1). Because the root measurements for plots with cheatgrass included roots of both the target individual and cheatgrass, we expected that treatment to have significantly greater root length density. Root length densities for individual depth increments within each treatment overlapped for both species throughout the soil profile, especially in 1987 (Fig. 2). Although differences among treatments in 1988 were larger than those in 1987, especially for plots with needle-and-thread grass as target individuals, the 3-way interaction term Treatment*Year*Depth was not significant for plots with either species at target individuals (Table 1).

Because the P value for the Treatment*Year*Depth from the ANOVA for needle-and-thread grass plots was low, we computed root length density for the entire 1.4-m-deep soil profile in order to integrate the 6 depth increments. Data were analyzed with a split-split plot ANOVA (Table 4a). For plots with rabbitbrush plants as target individuals, the Year*Location interaction term (Table 4b) confounded the significant Location subplot factor (Table 4c). Locations were not significantly different in 1987, but were significantly different in 1988. For plots with either native species as target individuals, the root length density for the soil profile in 1987 was significantly less than that in 1988 (Table 4d). However, all ANOVA terms that involved the whole-plot Treatment factor were not significant, even though mean root length density for the soil profile of plots with cheatgrass in the recently burned area tended to be slightly greater than that of other plots in 1988 (Fig. 3).

In order to focus only on the plots from the recently burned area, we reran the ANOVA's without data from the long-term

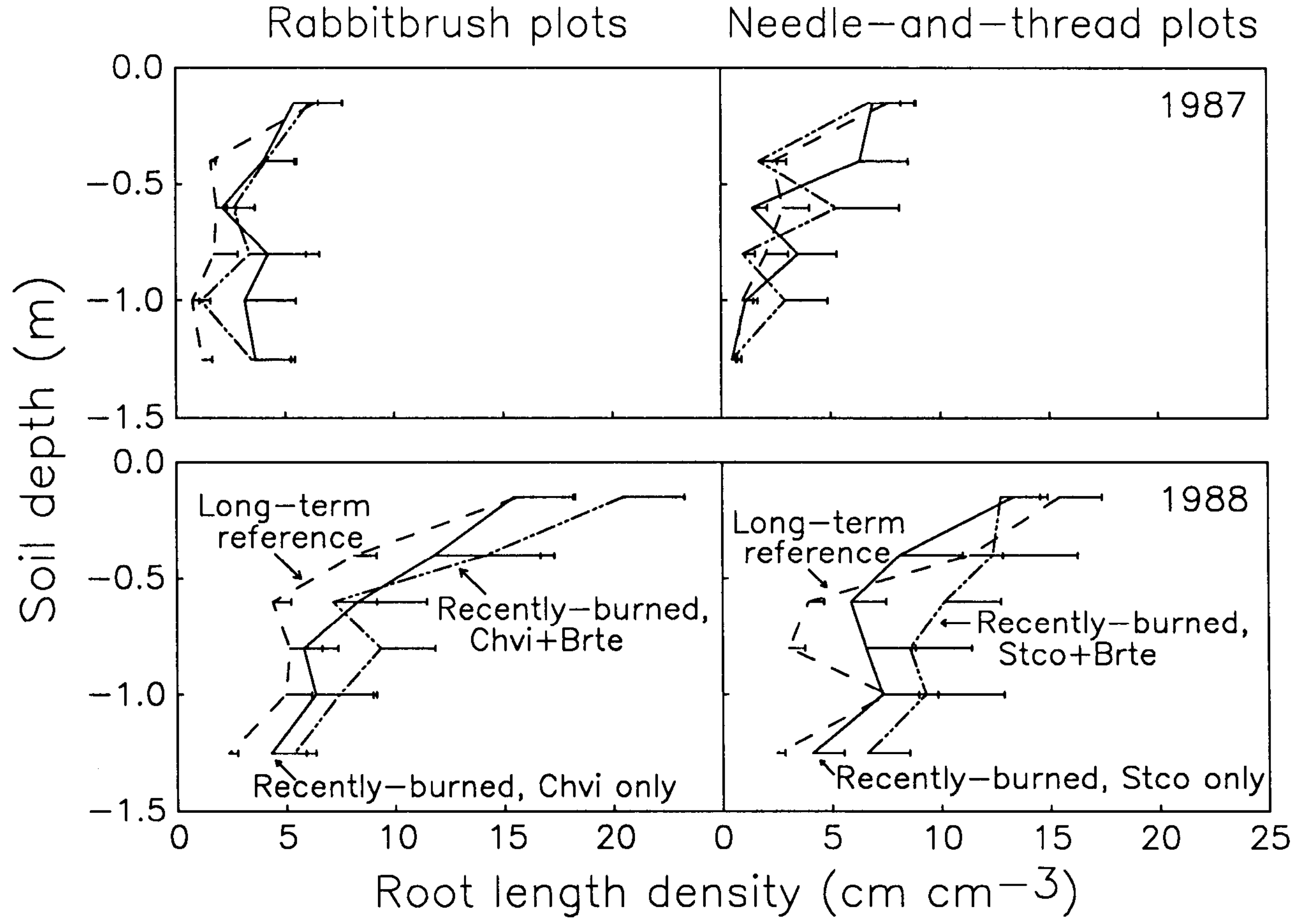

Fig. 2. Root length density at different depth increments for plots with rabbitbrush (Chvi) as the target individual (left frames) and plots with needle-and-thread grass (Stco) as the target individual (right frames). Upper frames are means from 1987, and lower frames are means from 1988. Solid lines are plots in the recently burned area without competition: dash-dot-dot lines are plots in the recently burned area with cheatgrass competition; and dashed lines are plots in the long-term reference area. Error bars are standard errors of the mean. At any 1 depth, treatment means within any 1 frame were not significantly different (see Table 1a).

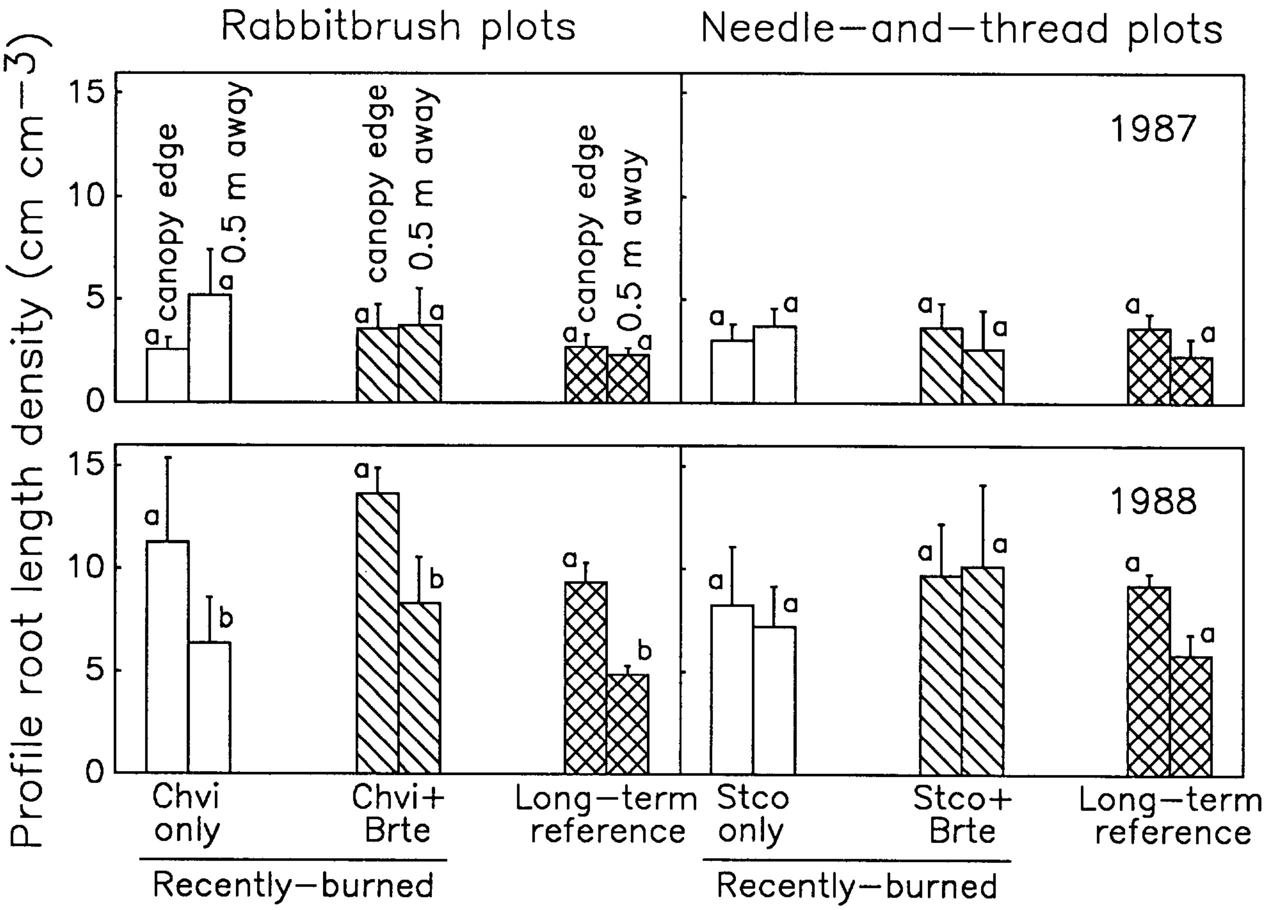

Fig. 3. Root length density for the entire soil profile from rabbitbrush (Chvi) plots (left frames) and needle-and-thread grass (Stco) plots (right frames) in 1987 (upper frames) and 1988 (lower frames). Open bars are plots in the recently burned area without competition; diagonal bars are plots in the recently burned area with cheatgrass competition; and crosshatch bars are plots in the long-term reference area. For each pair of bars, the left bar is mean root length density for soil cores taken at the edge of the target individual, and the right bar is that taken 0.5 m away from the edge of the canopy. Error bars are standard errors of the mean. With the exception of a significant Location effect in 1988 for rabbitbrush, means within a frame were not significantly different (see Table 2a).

reference area. Most of the significant terms in Tables 1 and 4a were again significant, and all the terms involving Treatment were, again, not significant (results not shown). We next removed the 1987 measurements from our data set and analyzed the data with split-plot types of ANOVA's, but all the ANOVA terms involving Treatment were still not significant.

Discussion

The roots system of cheatgrass and the native species compete. Evidence to support this statement is based upon the lack of statistical significance for any ANOVA terms that involved the whole-plot Treatment factor. If cheatgrass roots were not affecting root growth of the established perennial plants after fire, then the combined root length densities of the target species plus cheatgrass in plots with both species should have been greater than the root length densities of plots with only the target species. We also expected that this would be especially striking at 0.5 m from the edge of the target individuals. However, root length density of plots in the recently-burned area with only the target species were nearly identical to the combined root length density of plots with both the target species and cheatgrass in 1987 (Figs. 2 and 3). Small differences in mean root length density existed in 1988, but were not significant. We cannot unequivocally conclude from our data whether cheatgrass or the native species is the better competitor: we have evidence that cheatgrass reduces root length densities of the native species (relative to monocultures of the native species), but we do not know to what extent the native species reduce root length densities of cheatgrass (relative to cheatgrass monocultures). None-the-less, productivity and water status of both rabbitbrush and needle-and-thread grass were also adversely affected by cheatgrass (Melgoza et al. 1990). Because plants depend on their root systems to exploit the soil space around them, the results from our 2 studies suggest that the root system of cheatgrass utilized soil resources that otherwise would have been used by the native plants. Similar results were noted for competition between bluebunch wheatgrass and cheatgrass in growth chamber studies (Harris 1967).

Distribution of roots in the belowground space is important because root length density is closely related to uptake of water (Caldwell 1976, Lascano and van Bavel 1984) and nutrients (Silberbush and Baker 1985, Caldwell and Richards 1986). Water is the limiting factor in desert communities (Fowler 1986, Smith and Nowak 1990), and frequently water is present in limited amounts and space. Species growing together can avoid competition to some extent by having active roots at different depths, but root length density of all species in our study was greatest in the upper 0.5 m of soil, suggesting considerable root competition. Cheatgrass is very effective in removing soil water from the upper levels early in the spring (Cline et al. 1977, Melgoza et al. 1990), and competition between cheatgrass and native species in the upper soil layers

Table 4. Split-split plot analysis of variance (ANOVA) and mean comparisons for root length density (cm cm^{-3}) for the 1.4 m deep soil profile.

---------------------(a) ANOVA table---------------------

Source[1]	d.f.[2]	P values Chvi plots[3]	 Stco plots[4]
Treatment	2	0.343	0.526
Treatment*Plot (error)	21		
Year	1	0.000	0.000
Treatment*Year	2	0.589	0.677
Treatment*Year*Plot (error)	21		
Location	1	0.010	0.373
Treatment*Location	2	0.703	0.650
Year*Location	1	0.001	0.733
Treatment*Year*Location	2	0.652	0.757
Treatment*Year*Location*Plot (error)	42		
Total	95		

------------------(b) Mean comparisons for locations by year (Year*Location interaction term)---------------------------

Chvi plots:

Year	Canopy edge	0.5 m from edge
1987	3.0a[5]	3.8a
1988	11.4b	6.5a

----------(c) Mean comparisons for Location subplot factor----------

Chvi plots:

Canopy edge	0.5 m from edge
7.2b	5.1a

------------(d) Mean comparisons for Year subplot factor------------

	1987	1988
Chvi plots:	3.4a	9.0b
Stco plots:	3.2a	8.4b

[1] Sources of variation are: Treatment = whole-plot treatments of presence/absence of cheatgrass in recently-burned area and long-term reference; Year = 1987/1988; Location = edge of canopy/0.5 m from edge; Plot = experimental unit.
[2] Degrees of freedom
[3] ANOVA from plots with rabbitbrush (Chvi) as the target individual
[4] ANOVA from plots with needle-and-thread grass (Stco) as the target individual
[5] Mean comparisons were made with a L.S.D. test; means within a row that have the same letter did not differ significantly (P>0.05).

would be intense if both draw simultaneously upon a limited supply of soil resources. Whether competition between perennial plant roots and cheatgrass roots was restricted to the upper soil profile or also occurred in lower portions of the soil profile cannot be definitively determined from our results and would require a technique to positively differentiate roots of each species.

Fire did not have any short-term effects on root production. Mean root length densities of both treatments from the recently-burned area were not significantly different from means for the long-term reference area in either 1987 or 1988. Plant survival after fire has been related more to the capacity to rapidly utilize available soil water during the early stages of regrowth after fire, rather than to direct effects of fire (R. Robberecht, personal communication). Our results are consistent with this hypothesis: all species in our study area are relatively tolerant of late-summer fires, and their root systems appeared to explore the soil profile after fire to the same extent as plants that were not recently burned. Whether short-term root production of needle-and-thread grass burned in mid-summer, when it is more susceptible to damage (Wright and Klemmedson 1965), is reduced is not known, but would be a good test of this hypothesis.

Results from this study enhance our understanding of the belowground competitive interactions of native species and cheatgrass after fire. Rapid root development and an extensive fibrous root system have been implicated as characteristics that make cheatgrass a vigorous colonizer (Harris 1977) and enhance its ability to rapidly occupy the open spaces created by the removal of fire-intolerant plants on sagebrush sites (Thill et al. 1984, Young et al. 1969). Our studies also indicate that cheatgrass successfully competes with established native perennials (Melgoza et al. 1990) and partially reduces the root systems of native species. Competition from cheatgrass has important long-term implications. If stands of cheatgrass become established in sagebrush communities after fire, the cheatgrass stands may not only resist invasion by perennials (Harris 1967), but may also partially displace the perennial plants that survive the fire.

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