

EFFECTS OF NUTRIENT PATCHES AND ROOT SYSTEMS ON THE CLONAL PLASTICITY OF A RHIZOMATOUS GRASS

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Abstract. Clonal plant foraging has been examined primarily on individual clones exposed to resource-poor and resource-rich environments. We designed an experiment to examine the clonal foraging behavior of the rhizomatous grass *Elymus lanceolatus* ssp. *lanceolatus* under the influence of neighboring plant root systems in a heterogeneous nutrient environment. Individual *Elymus* clones were planted in large bins together with one of three neighboring grass species, *Agropyron desertorum*, *Pseudoroegneria spicata*, or *Bromus tectorum*, which differ in rooting density and growth activity. The position of *Elymus* clones was manipulated so rhizomes encountered a short-duration nutrient patch and subsequently root systems of the neighboring plants. Unexpectedly, the morphological plasticity of the perennial grass *Elymus lanceolatus* ssp. *lanceolatus* was influenced by the presence of the neighboring species much more than by the local nutrient enrichments, although nutrient patches did amplify some of the foraging responses. *Elymus* rhizomes branched readily and initiated large daughter plants as they encountered the low-density root systems of *Pseudoroegneria*. When *Elymus* encountered the fine, dense root systems of the annual *Bromus*, clonal expansion was initially reduced. Yet, after the short growing season of *Bromus*, *Elymus* resumed clonal expansion and produced several daughter plants. *Elymus* clones were most constrained by the fine, dense root systems of *Agropyron desertorum*. In this case, a few, long rhizomes avoided the densely rooted soil environment by growing aboveground as stolons crossing over the *Agropyron* tussocks. *Elymus* clonal biomass was largest in neighborhoods of *Pseudoroegneria*, intermediate in neighborhoods with *Bromus*, and smallest in neighborhoods with *Agropyron*. The latter were approximately half the size of those in the *Pseudoroegneria* environments. *Elymus* growth could not be explained by simple resource competition alone; other mechanisms must have been involved in the apparent differences in interference patterns of neighboring plants with *Elymus*.

Key words: clonal plant morphology; competition; *Elymus lanceolatus* ssp. *lanceolatus*; morphological plasticity; plant foraging; plant interference; rhizomes; root systems; soil heterogeneity.

INTRODUCTION

Horizontal expansion and exploratory growth of rhizomes expose individual clones to spatial variation in their habitats (Snaydon 1962). Environmental variation in a plant community consists of both the heterogeneous distribution of abiotic resources such as water, nutrients, light, and available space, and biotic features such as competition and facilitation by neighboring plants (Turkington and Harper 1979, Burdon 1980, Aarssen 1983, Schmid 1985, Goldberg 1990, Jackson and Caldwell 1993a, b, Hacker and Bertness 1995). Empirical and theoretical studies suggest that clonal plants may discriminate between low and high quality habitats in heterogeneous nutrient environments by various expressions of morphological plasticity de-

scribed as clonal foraging (Slade and Hutchings 1987a, b, Sutherland and Stillman 1988). Clones pass through resource-poor sites with minimal investment of biomass in spacer organs (rhizomes, stolons). Yet, in resource-rich sites, clones may have relatively short spacer organs and increase rhizome branching.

However, not all clonal species are plastic and forage in the same way (de Kroon and Knops 1990, de Kroon and Hutchings 1995, Dong et al. 1996). Architectural constraints may reduce plastic clonal responses (Waller and Steingraeber 1985, Schmid 1986, Carlsson et al. 1990, Schmid and Bazzaz 1992, Newton and Hay 1996). Physical obstacles or vigorous competitive neighbors may suppress growth completely (Schmid and Bazzaz 1992, Evans and Cain 1995).

Biotic and abiotic influences on growth and morphology of clonal plants are prevalent in plant communities. However, the effects of biotic and abiotic influences on clonal foraging behavior have been rarely examined simultaneously. It is generally assumed that plants respond similarly to abiotic and biotic factors,

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in that resource depletion by a plant neighbor is equivalent to low resource availability (Schmid 1985, Eriksson 1986, Evans and Cain 1995, Price and Hutchings 1996). There is increasing evidence, however, that neighboring plant root systems may influence a plant's morphology by interference mechanisms other than the low resource amounts caused by the competitor (Mahall and Callaway 1991, 1996, Turkington et al. 1991, Krannitz and Caldwell 1995, Huber-Sannwald et al. 1996, Huber-Sannwald et al. 1997). Mahall and Callaway (1991) showed that root growth of neighboring plants might be slowed by diffusible root exudates that were not species specific in character, or by species-specific reactions that required root contact but did not involve diffusible inhibiting substances.

Some questions regarding the functional interpretation of morphological plasticity in clonal growth are pertinent in this context. (1) Is phenotypic plasticity functionally important only for foraging for nutrients, and competing with neighboring plants, or, is it also important for circumventing physical obstacles such as stones or the root systems of neighboring plants? (2) Do root systems of different neighboring species present similar barriers to a clonal plant or do these barriers differ among neighboring species and, therefore, elicit different morphological responses by the clonal plant? (3) If there are differences in the nature of barriers presented by different neighboring species, is this due primarily to the density of the root system, to the timing of active growth and resource acquisition by these neighbors, or to other species-specific characteristics such as resource acquisition capacity, root exudates, or mycorrhizal influences?

To address the above questions, we tested how root systems of co-occurring perennial and annual grasses from the intermountain sagebrush-steppe in North America affect the morphological plasticity and growth of the rhizomatous perennial grass *Elymus lanceolatus* ssp. *lanceolatus* (Scribner and J. G. Smith) Gould (thickspike wheatgrass). In a previous study (Humphrey and Pyke 1997), *Elymus* exhibited foraging behavior by plasticity in the placement of ramets, i.e., more densely packed tillers were located in high nutrient patches. We were interested in taking the next step by examining how a heterogeneous nutrient distribution affects *Elymus* clonal responses in the presence of other species. We expected that rhizomes would penetrate coarse, low-density root systems of the native *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) and short-lived, fine root systems of the exotic annual *Bromus tectorum* L. (cheatgrass), but would be less effective in penetrating the perennial, dense root systems of the introduced *Agropyron desertorum* (Fisch. ex Link) Schult (crested wheatgrass) (Caldwell and Richards 1986). Several species of the Great Basin are capable of exploiting nutrients in enriched soil patches through rapid increases in root proliferation and uptake capacity (Jackson and Caldwell

1989, Jackson et al. 1990, Caldwell et al. 1991). They also can rapidly acquire nitrogen from nitrogen pulses of very short duration (Bilbrough and Caldwell 1997) suggesting that these plants may be well adapted to ephemeral, local nutrient pulses that may occur frequently in arid environments (Chapin 1988, Robinson 1994, Bilbrough and Caldwell 1997). Therefore, we examined how a short-duration nutrient supply would affect clonal foraging in *Elymus*. Finally, we compared two genets of *Elymus* in response to these biotic and abiotic factors because genetic variation may contribute to differences in morphological plasticity of clonal plants. By combining a heterogeneous nutrient distribution and root system interference by different, yet common coexisting species, this experimental setting represented situations one might expect in natural plant communities.

METHODS

Experimental design

In autumn of 1993, 39 circular fiber bins (76 cm depth \times 80 cm diameter) were arranged equidistant from each other in a field near Logan, Utah, USA (41°45' N, 111°48' W; 1460 m elevation). Bins were filled with a 1:1 mixture of sand and nutrient-depleted sandy loam with low nitrogen (<5 mg/kg) and phosphorus (<3 mg/kg) commonly found in the sagebrush steppe (Jackson and Caldwell 1991). We examined the effects of three experimental factors (barrier species, constraint environment, fertilization) on *Elymus* morphological properties and clonal biomass.

Each bin was divided radially into six sections by two pairs of long (20 cm) and of short (10 cm) walls made of galvanized metal sheets (1 mm thick). These walls were inserted into the soil to a depth of 30 cm so that each pair radiated from the *Elymus* plant toward the barrier plant (Fig. 1). The walls served to direct rhizome growth toward the nutrient patches and the barrier plant root systems.

The presence and absence of barrier plants in combination with walls of different lengths created three environments of different constraints (CON) to manipulate the lateral growth of rhizomes and the intensity of neighbor plant root density in each section (see Fig. 1). Rhizomes were forced to encounter the barrier plants in the full-constraint environment and were encouraged, but not forced, to do so in the partial-constraint environment. Roots of the barrier plants in sections with full- and partial-constraint environments could proliferate into sections with minimal constraints. The purpose of the minimal-constraint environment was to provide a control treatment with very reduced densities of neighboring plant roots in the immediate vicinity of *Elymus*. The density, and thus the potential resistance, of barrier plant roots was greatest in the full-constraint environment, less in the partial-

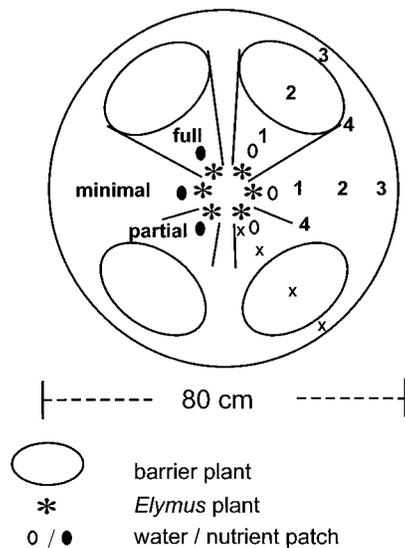


FIG. 1. Experimental design within bins (main plots). Each bin was assigned one of three barrier species *Agropyron*, *Pseudoroegneria*, or *Bromus*. A bin consisted of six treatment sections of equal size (subplots), separated by metal walls. Six *Elymus* mother plants were planted in a circular area of 10-cm diameter in the center of the bin. Barrier plants were present in four sections and absent in two sections. Each section was assigned to one constraint (full/partial/minimal) and one fertilization (water control/nutrient patch) treatment. Constraint environments are labeled in three sections on the left side of the figure. Three sections received nutrient patches (indicated by solid circles on the left side of the figure), and the other three received water patches (indicated by open circles on the right side of the figure) 5 cm from the mother plant in the direction of the barrier plants and 4 cm below the soil surface. Four zones were designated in sections with barrier plants; these zones are indicated with numbers in the three sections on the right side of the figure. Zone 1 comprised the area between the mother and the barrier plants. Zone 2 included the area in the densest part of the barrier plant root system. Zone 3 was the area behind the barrier plants. Zone 4 was the area where rhizomes circumvented or attempted to circumvent barrier plants in the sections with partial and full constraints, respectively. In sections with minimal constraints, three zones were designated corresponding to Zones 1, 2, and 3 of the sections with barrier plants. The "x"-symbol in one section represents the location where root cores were taken for root density estimates.

constraint environment, and much less, though present, in the minimal-constraint environment.

Thirteen bins were assigned to each of three barrier species (SPP). Barrier plants were located 10 cm from the edge and 15 cm from the center of the bin; each barrier plant occupied an area of ~ 20 by 8 cm (see Fig. 1). In March 1994, 15 seeds of *Bromus tectorum*, an annual species with high rooting density, were sown in two adjacent circular areas (~ 8 cm diameter) and represented one "barrier plant." In early April, 52 5-yr-old tussocks of *Agropyron desertorum*, a perennial species with high rooting density, and *Pseudoroegneria spicata*, a perennial species with low rooting density (Caldwell and Richards 1986), were excavated from a

nursery at the same field site. Although the rooting densities differ between the two perennial species, both grasses have similar lateral extension of their root systems (Caldwell and Richards 1986) and exhibit similar root nutrient uptake capacity (Jackson et al. 1990, Caldwell et al. 1991). Each tussock was divided into two parts that were planted next to each other to create one "barrier plant."

In May, two genets of the rhizomatous *Elymus lanceolatus* ssp. *lanceolatus* were randomly chosen from a 6-yr-old nursery at the same field site. For each barrier species, Genet 1 (GEN 1) was planted in seven bins and Genet 2 (GEN 2) in the other six bins. We planted one *Elymus* plant, hereafter referred to as the mother plant, in each section close to the center of each bin, thus forming a circle of six mother plants with a diameter of ~ 10 cm (Fig. 1). Mother plants consisted of two or three equally sized shoots with two elongated rhizomes (2–4 cm long). They were planted with their rhizomes directed toward the barrier plants.

The fertilization treatments (FERT) were applied in mid-May, 2 wk after transplantation of the *Elymus* plants. Within a bin, three sections received nutrient patches and three received control patches (Fig. 1). The patches were placed only 5 cm from the mother plants to maximize the probability that rhizomes would encounter them. Nutrient patches consisted of 10 mL of highly concentrated fertilizer solution (8.8 g Miracle-Gro, Sterns, Port Washington, New York, per liter distilled water; 40 mmol $\text{NH}_4\text{H}_2\text{PO}_4$, 25 mmol $\text{CH}_4\text{N}_2\text{O}$, 25 mmol K_2O , plus trace elements). Control patches were injections of 10 mL of distilled water. These patches were injected only once to represent a short-duration nutrient supply. The controls for nutrient patches were water patches in the same biotic environment. In the full-constraint environments, we expected *Elymus* to be more responsive to the growth constraints of the massive root systems than to the nutrient patches. Whereas in the minimal-constraint environments, we expected *Elymus* to be more responsive to the nutrient patches, since a smaller growth constraint was present.

Inflorescences of *Elymus* mother plants were removed continuously to promote vegetative growth (Loomis 1953). Five days after the patches were injected, bins were regularly watered every fourth day until July 1994 and once a week thereafter. Starting in June 1994, all mother plants of *Elymus* were supplied with a total of 300 mL of a diluted fertilizer solution (0.8 g Miracle-Gro per liter distilled water) once a month for 3 mo. The amount of nutrients that each mother plant received was very small compared to the nutrient patch; we doubt that there was any significant acropetal nutrient transport from the mother plant towards the rhizome tip that may have interfered with local foraging responses. The experiment lasted 6 mo covering the main growth periods for *Elymus* rhizomes

in late spring and fall. Plants were harvested from late October until mid-November.

Response variables

We measured elements of *Elymus* clonal morphology and clonal biomass to evaluate *Elymus* clonal foraging and competitive interaction between *Elymus* and the barrier species, respectively. During the growing season, emerging daughter ramets were counted and labeled with colored wires to differentiate between summer and fall tillers. Shoots of mother plants and daughter ramets were harvested for biomass estimates in October 1994. Total *Elymus* clone biomass was computed as the sum of mother shoots, daughter ramets, and rhizome mass. It was not feasible to separate roots of *Elymus* plants from roots of the barrier species; thus root biomass estimates of *Elymus* mother plants are not available. We expected the barrier species to be better competitors than *Elymus*, simply because they were substantially larger than the *Elymus* at the beginning of the experiment.

Both growth (aboveground biomass) and morphological responses of *Elymus* were expected in the various treatment combinations. Growth responses might be indicative of stimulation by nutrient acquisition from the patches or resource competition by the different neighbor species. Morphological responses in the absence of growth changes may signify nutrient foraging or reactions to neighbors that do not involve immediate resource competition.

To determine root density (centimeter root length per cubic centimeter soil volume) in the different constraint environments, prior to harvest we excavated four soil cores in each section (top 10 cm; 30 cm³ each; Fig. 1): one adjacent to *Elymus* plants, one near the barrier plant, one in the barrier plant, and one behind the barrier plant. In sections without barrier plants, soil cores were taken at equivalent locations. Soil cores were sieved to extract roots and total root length was determined with a root length scanner (Comair, Incorporated, Melbourne, Australia). Although roots of the barrier species could not be separated from those of *Elymus*, comparison of root densities in sections with barrier plants to densities in sections without barrier plants provides a relative estimate of the potential growth barriers presented by the roots of these different barrier species.

A high-pressure water stream was used to wash away the soil and expose rhizomes in the bin. Rhizomes were classified as first- and second-order rhizomes and were counted. First-order rhizomes grow from basal lateral buds of mother plants. We calculated the proportion of first-order rhizomes that reached different zones in each section. *Elymus* rhizomes that remain close to the mother plants (Fig. 1; Zone 1) would indicate exploitation of a favorable site; those that extend away from the mother plant (Fig. 1; Zones 2, 3, 4) would indicate exploration for new sites. The proportion of first-order

rhizomes reaching different zones is an approximation of net displacement, sensu Cain (1991, 1994). Second-order rhizomes grow from lateral buds along first-order rhizomes and give an estimate of lateral rhizome branching. Proportion of branching nodes was computed as the number of second-order rhizomes divided by the total number of nodes of first-order rhizomes for each mother plant. Each rhizome was mapped from its base to its tip on acetate sheets overlying a plexiglass mapping table. Maps provided visual reference for rhizome distributions. Rhizomes that were inadvertently damaged during the process of excavating soil cores were eliminated from statistical analyses. All rhizomes were harvested, and the length of each first-order rhizome was recorded. Mean rhizome length was computed over all first-order rhizomes for each section of a bin. Rhizome samples were oven-dried (48 h at 75°C) for estimations of total rhizome biomass.

Statistical analysis

For each response variable, the statistical model was an analysis of variance of a four-way factorial in a split-plot design, with bins containing a single barrier species as main plots and sections within bins as subplots. Barrier species (*Agropyron/Pseudoroegneria/Bromus*) and genotype (GEN 1/GEN 2) were fixed effects assigned in an unbalanced two-way factorial to the main plots. Constraint (full/partial/minimal) and nutrient (control/fertilization) treatments were fixed effects assigned in a two-way factorial to the six sections within a bin.

For number of first-order rhizomes, proportion of branching rhizomes, number of daughter ramets (total, summer, and fall), and total *Elymus* clonal biomass, data were summed over all zones within a section. The proportion of first-order rhizomes reaching a given zone (Fig. 1) was examined in a separate analysis for each of the four zones. Root density data were pooled over genotypes. Root density at each sampling location was examined in a separate analysis for each location. For each analysis, residuals from the model were examined for normality. We conducted a posteriori mean comparison tests for significant main effects and interactions using Bonferroni-adjusted *P* values.

The number of first-order rhizomes, the proportion of first-order rhizomes reaching different zones, and the number of daughter ramets in summer were analyzed on their original scales. Other response variables were transformed to better meet analysis assumptions. Arcsine square-root transformation was applied to the proportion of branching nodes and square-root transformation to mean first-order rhizome length. Log transformation ($\log(x + 1)$) was applied to number of daughter ramets (total, fall), total *Elymus* clone biomass, and root density. All analyses were computed using the MIXED procedure in SAS Release 6.11 (SAS Institute 1988).

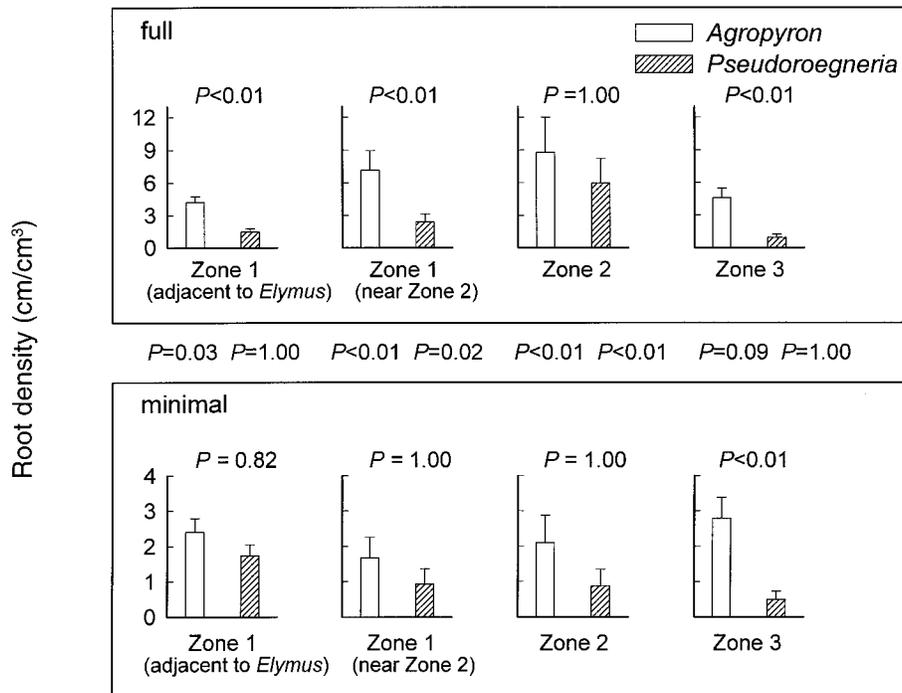


FIG. 2. Least-squares means (± 1 SE) (backtransformed from the log scale) of root density in *Agropyron* and *Pseudoroegneria* bins at four locations at 10-cm depth in sections with full-constraint (top) and minimal-constraint (bottom) environments. In the full-constraint environment (top) the plots, from left to right, are for the following locations: adjacent to *Elymus* plants (in Zone 1), near barrier plants (in Zone 1), in the center of barrier plants (Zone 2), and behind barrier plants (Zone 3). In the minimal-constraint environment where there were no barrier plants (bottom), the locations correspond to the same positions as in the full-constraint environment (top). The Bonferroni-adjusted *P* values above each graph refer to the significance levels for the comparisons between the two barrier species at a given location (i.e., the simple effect of barrier species in the full- or minimal-constraint environment). The Bonferroni-adjusted *P* values between the top and bottom plots are significance levels for the comparisons between the two constraint environments (full/minimal) for *Agropyron* or *Pseudoroegneria* in each zone (i.e., the simple effect of constraint environment for a given barrier species). The results for the partial-constraint environment are not depicted, since there was no statistical difference between full- and partial-constraint environments. Fertilization had no effect on root density.

RESULTS

Root density

Only root densities in *Pseudoroegneria* and *Agropyron* bins were compared, since the majority of *Bromus* roots were decomposed by the time of harvest. In the full- and partial-constraint environments, root density in *Agropyron* bins was significantly greater than root density in *Pseudoroegneria* bins in all locations but Zone 2. In minimal-constraint environments, root densities were similar in the *Agropyron* and *Pseudoroegneria* bins, except in Zone 3, where root density was greater in *Agropyron* than in *Pseudoroegneria* bins (Fig. 2; Table 1). In *Agropyron* bins, the full- and partial-constraint environments had greater root densities than minimal-constraint environments. In *Pseudoroegneria* bins, however, the full- and partial-constraint environments had greater root densities than minimal-constraint environments only around Zone 2 (Fig. 2; Table 1).

Clonal morphology and manifestation of foraging

Mean first-order rhizome length of *Elymus* was affected by the nutrient patches, but the effect depended on barrier species and type of constraint (Fig. 3; Table 2, SPP \times CON \times FERT interaction). Fertilization led to longer rhizomes compared to controls (water patch) only in *Agropyron* bins, in sections without barrier plants. Rhizomes were significantly shorter in fertilized sections with *Agropyron* than without *Agropyron* barrier plants. In *Bromus* bins, rhizomes were shorter in sections with barrier plants than without barrier plants. None of the treatments affected *Elymus* rhizome length in *Pseudoroegneria* bins. Overall, rhizomes were longer in bins with the two perennials than in those with the annual grass (Table 2, SPP main effect). Both genotypes had similar lengths of first-order rhizomes (Table 2)

Unexpectedly, the proportion of rhizomes, regardless of length, that remained close to *Elymus* mother plants (Zone 1) presumably to exploit resources, was affected

TABLE 1. ANOVA of root density examining the effects of barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
1) Zone 1 adjacent to <i>Elymus</i>			
Species (SPP)	1, 8	19.17	0.002
Constraint (CON)	2, 40	1.41	0.256
SPP × CON	2, 40	3.30	0.048
Fertilization (FERT)	1, 40	0.00	0.974
SPP × FERT	1, 40	1.60	0.213
CON × FERT	2, 40	2.61	0.086
SPP × CON × FERT	2, 40	1.11	0.340
2) Zone 1 near barrier plant			
SPP	1, 8	8.03	0.022
CON	2, 40	24.66	0.001
SPP × CON	2, 40	2.56	0.090
FERT	1, 40	3.86	0.056
SPP × FERT	1, 40	0.28	0.598
CON × FERT	2, 40	0.82	0.446
SPP × CON × FERT	2, 40	0.84	0.440
3) Zone 2			
SPP	1, 8	1.58	0.244
CON	2, 40	36.20	0.001
SPP × CON	2, 40	0.09	0.917
FERT	1, 40	1.53	0.223
SPP × FERT	1, 40	3.98	0.053
CON × FERT	2, 40	0.44	0.647
SPP × CON × FERT	2, 40	0.83	0.445
4) Zone 3			
SPP	1, 8	34.46	0.001
CON	2, 40	5.08	0.012
SPP × CON	2, 40	0.51	0.603
FERT	1, 40	1.44	0.237
SPP × FERT	1, 40	0.11	0.737
CON × FERT	2, 40	2.82	0.072
SPP × CON × FERT	2, 40	3.07	0.058
Variance component estimates			
Variance component	df	Estimate	SE
1) Zone 1 adjacent to <i>Elymus</i>			
Pot (SPP)	8	0.008	0.013
Residual	40	0.105	0.023
2) Zone 1 near barrier plant			
Pot (SPP)	8	0.107	0.068
Residual	40	0.171	0.038
3) Zone 2			
Pot (SPP)	8	0.230	0.145
Residual	40	0.351	1.078
4) Zone 3			
Pot (SPP)	8	0.044	0.032
Residual	40	0.123	0.027

Note: The model is a three-way factorial in a split-plot design. Data were log-transformed (log (x + 1)) prior to analysis.

by the barrier species and constraint environments, but not by the nutrient patches (Fig. 4; Table 3, SPP × CON interaction). In *Bromus* and *Agropyron* bins, >50% and ~40% of the rhizomes, respectively, remained in Zone 1 regardless of constraint environments. In *Pseudoroegneria* bins, however, proportionally twice as many rhizomes (~60%) remained in Zone

1 in sections without barrier plants than in sections with barrier plants. Overall, the proportion of rhizomes remaining in Zone 1 was greater in bins with the annual grass than with the two perennials (Table 3, SPP main effect).

The proportion of exploring rhizomes that reached Zone 3 was affected by barrier species, fertilization, and constraint environments (Fig. 4; Table 3, SPP × CON × FERT interaction). In minimal-constraint environments of *Agropyron* bins, significantly more rhizomes reached Zone 3 under fertilized than under control conditions. In *Bromus* and *Pseudoroegneria* bins, fertilization did not affect the number of rhizomes reaching Zone 3 in any constraint environment. Proportionally two to three times more rhizomes reached Zone 3 in sections without barrier plants than in sections with barrier plants (Table 3; CON main effect).

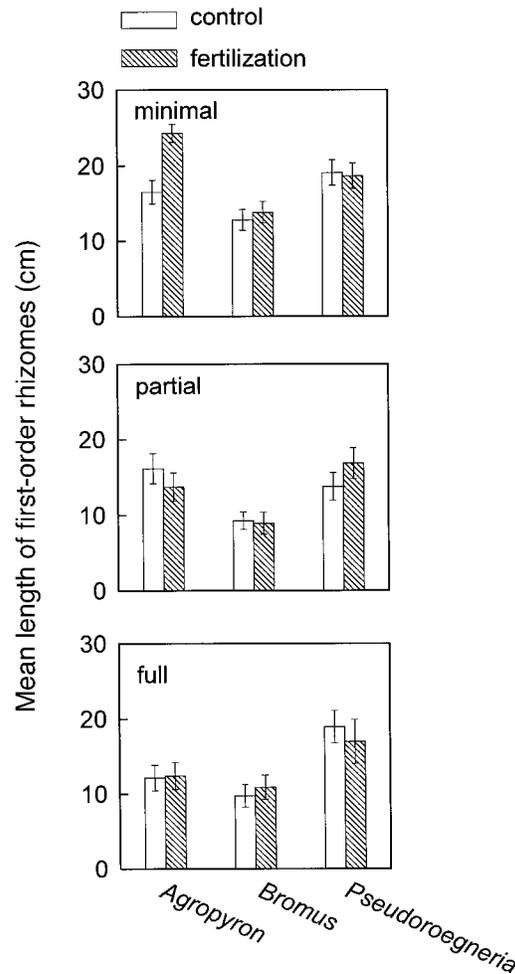


FIG. 3. Least-square means (± 1 SE) (back-transformed from the square-root scale) of mean first-order rhizome length of *Elymus* under fertilized (nutrient patch) and control (water patch) treatments in full-, partial-, and minimal-constraint environments for each of the three barrier species, *Agropyron*, *Bromus*, and *Pseudoroegneria*.

TABLE 2. ANOVA of mean first-order rhizome length of *Elymus* examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
Genotype (GEN)	1, 33	0.00	0.959
Species (SPP)	2, 33	9.93	0.001
GEN × SPP	2, 33	0.34	0.712
Constraint (CON)	2, 241	17.17	0.001
GEN × CON	2, 241	1.48	0.231
SPP × CON	4, 241	2.67	0.033
GEN × SPP × CON	4, 241	0.69	0.600
Fertilization (FERT)	1, 241	1.19	0.277
GEN × FERT	1, 241	0.01	0.923
SPP × FERT	2, 241	0.23	0.791
GEN × SPP × FERT	2, 241	0.14	0.865
CON × FERT	2, 241	1.47	0.232
GEN × CON × FERT	2, 241	0.92	0.340
SPP × CON × FERT	4, 241	2.43	0.049
GEN × SPP × CON × FERT	4, 241	3.15	0.025
Variance component estimates			
Variance component	df	Estimate	SE
Pot (GEN × SPP)	33	0.178	0.065
Residual	241	0.661	0.060

Note: The model is a four-way factorial in a split-plot design. Data were square-root transformed prior to analysis.

There was no difference between the two genotypes in the proportion of rhizomes reaching different zones.

None of the root barriers completely stopped rhizome growth in the zone of greatest root density (Fig. 4; Zone 3, full constraint). Similar proportions of rhizomes penetrated (Zone 2) as circumvented (Zone 4) the root systems in the full- and partial-constraint environments for all barrier species (Fig. 4; Zone 2 and 4; not statistically tested). However, 20% more *Elymus* rhizomes entered the zone of highest root density (Zone 2) of *Pseudoroegneria* than of *Bromus* plants. Most of the rhizomes that penetrated *Agropyron* plants actually emerged from the soil as they reached the tussocks and grew as "stolons," crossing the barrier plants above ground in the crowns of the tussocks.

Of all treatments, barrier species had the most pronounced effect on rhizome initiation in *Elymus* mother plants (Fig. 5 inset; Table 4, SPP main effect). *Pseudoroegneria* environments allowed the greatest activation of first-order rhizomes, *Agropyron* allowed only half as many, and *Bromus* an intermediate number. Overall, fertilization increased the number of first-order rhizomes (Fig. 5 inset; Table 4, FERT main effect). Both genotypes had similar numbers of first-order rhizomes (Table 4).

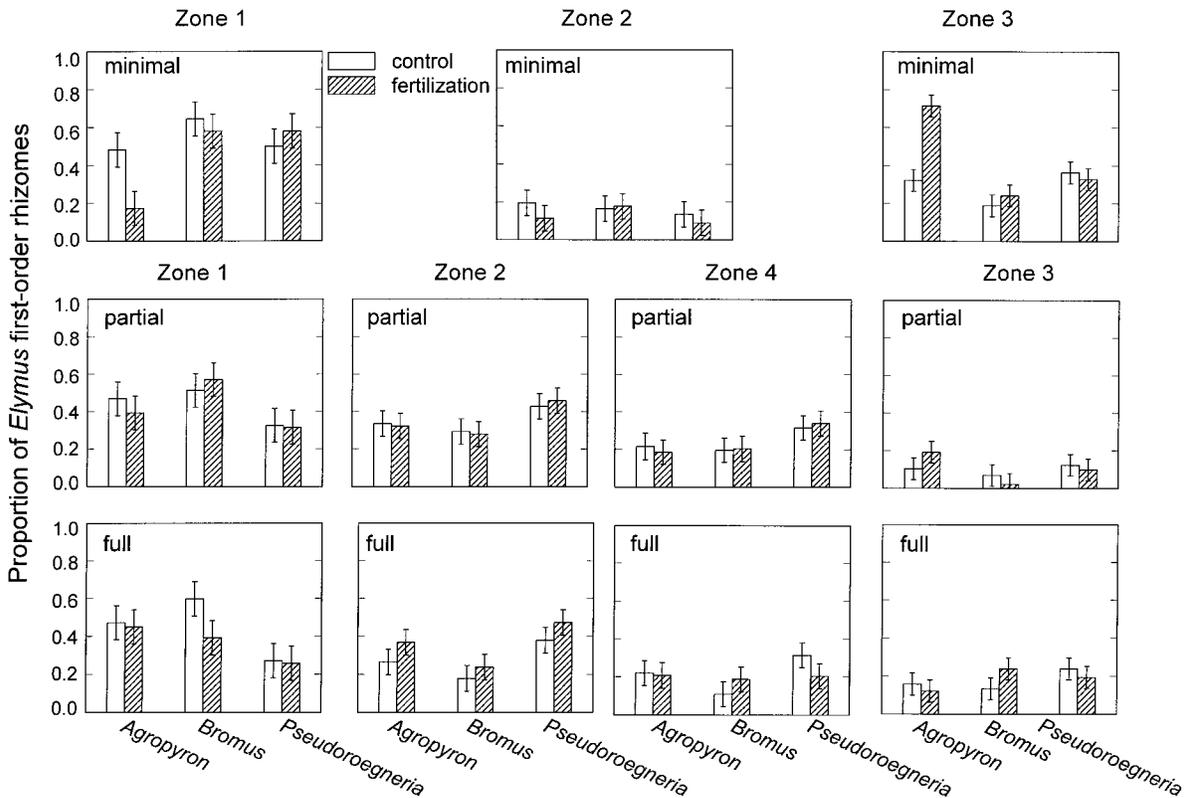


FIG. 4. Proportion of first-order rhizomes of *Elymus* (least-squares mean \pm 1 SE) that extended into different zones (see Fig. 1) away from mother plants. This variable was used as an indicator of net displacement of rhizomes in sections with minimal-constraint (top), partial-constraint (middle), and full-constraint (bottom) environments for the three barrier species and for the two nutrient treatments.

TABLE 3. ANOVA of proportion of first-order rhizomes of *Elymus* reaching Zones 1 and 3 examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects Source of variation	Zone 1			Zone 3		
	df	F	P	df	F	P
Genotype (GEN)	1, 33	1.01	0.323	1, 33	0.51	0.480
Species (SPP)	2, 33	4.11	0.026	2, 33	3.71	0.035
GEN × SPP	2, 33	0.08	0.928	2, 33	0.25	0.779
Constraint (CON)	2, 165	1.67	0.192	2, 165	37.68	0.001
GEN × CON	2, 165	0.74	0.477	2, 165	0.29	0.750
SPP × CON	4, 165	3.30	0.013	4, 165	5.74	0.001
GEN × SPP × CON	4, 165	0.15	0.962	4, 165	0.89	0.471
Fertilization (FERT)	1, 165	2.44	0.120	1, 165	3.97	0.048
GEN × FERT	1, 165	3.51	0.063	1, 165	1.35	0.247
SPP × FERT	2, 165	1.25	0.288	2, 165	4.49	0.013
GEN × SPP × FERT	2, 165	0.29	0.748	2, 165	0.51	0.601
CON × FERT	2, 165	0.46	0.631	2, 165	2.99	0.053
GEN × CON × FERT	2, 165	1.22	0.298	2, 165	1.12	0.330
SPP × CON × FERT	4, 165	1.28	0.278	4, 165	3.34	0.012
GEN × SPP × CON × FERT	4, 165	1.97	0.102	4, 165	2.16	0.076

Variance component estimates Variance component	Zone 1			Zone 3		
	df	Estimate	SE	df	Estimate	SE
Pot (GEN × SPP)	33	0.012	0.007	33	0.007	0.003
Residual	165	0.093	0.010	165	0.036	0.004

Note: The model is a four-way factorial in a split-plot design. Data were analyzed on the original scale. Zones were analyzed separately.

The proportion of second-order rhizome branching of *Elymus* depended on barrier species and fertilization (Fig. 5; Table 5, SPP × FERT interaction). Second-order rhizome branching occurred almost exclusively in *Pseudoroegneria* bins where fertilization caused more than a doubling of second-order rhizomes. Overall, the number of second-order rhizomes was not a function of the number of nodes or length of first-order rhizomes. Second-order branching occurred almost exclusively on one or two first-order rhizomes regardless

of the total number of first-order rhizomes. Rhizomes of GEN 2 branched proportionally twice as often than did GEN 1 (Table 5, GEN main effect).

The initiation of daughter ramets by *Elymus* depended on barrier species, constraint environment, and fertilization (Fig. 6, left side; Table 6, SPP × CON × FERT interaction). In the minimal-constraint environments, the number of daughter ramets increased with fertilization compared to controls in *Bromus* bins; however it decreased in *Agropyron* bins. In the full-con-

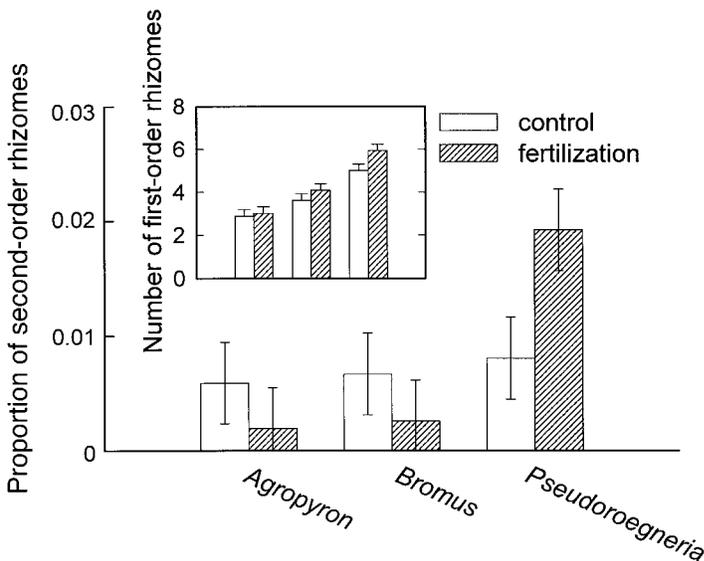


FIG. 5. Least-squares means (± 1 SE) (back-transformed from the arcsine square-root scale) of proportion of second-order rhizomes of *Elymus* for the barrier species *Agropyron*, *Bromus*, and *Pseudoroegneria* under fertilized (nutrient patch) and control (water patch) conditions. Inset: Least-squares means (± 1 SE) of number of first-order rhizomes of *Elymus* for the barrier species *Agropyron*, *Bromus*, and *Pseudoroegneria* under fertilized (nutrient patch) and control (water patch) conditions.

TABLE 4. ANOVA of number of first-order rhizomes of *Elymus* examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
Genotype (GEN)	1, 33	0.04	0.844
Species (SPP)	2, 33	29.05	0.001
GEN × SPP	2, 33	2.45	0.101
Constraint (CON)	2, 165	2.82	0.063
GEN × CON	2, 165	0.84	0.432
SPP × CON	4, 165	0.43	0.787
GEN × SPP × CON	4, 165	1.93	0.241
Fertilization (FERT)	1, 165	5.07	0.026
GEN × FERT	1, 165	1.41	0.237
SPP × FERT	2, 165	1.04	0.357
GEN × SPP × FERT	2, 165	0.76	0.468
CON × FERT	2, 165	1.34	0.267
GEN × CON × FERT	2, 165	0.03	0.971
SPP × CON × FERT	4, 165	1.64	0.167
GEN × SPP × CON × FERT	4, 165	0.51	0.728
Variance component estimates			
Variance component	df	Estimate	SE
Pot (GEN × SPP)	33	0.230	0.187
Residual	165	2.975	0.328

Note: The model is a four-way factorial in a split-plot design. Data were analyzed on the original scale.

straint environments in *Agropyron* bins, fertilization resulted in more daughter ramets than controls. In *Pseudoroegneria* bins, the initiation of daughter ramets did not differ between sections. GEN 2 developed more daughter ramets than did GEN 1 (Table 6, GEN main effect).

TABLE 5. ANOVA of proportion of second-order rhizomes of *Elymus* examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
Genotype (GEN)	1, 33	8.78	0.006
Species (SPP)	2, 33	7.28	0.002
GEN × SPP	2, 33	1.26	0.300
Constraint (CON)	2, 165	1.15	0.318
GEN × CON	2, 165	1.02	0.363
SPP × CON	4, 165	0.73	0.574
GEN × SPP × CON	4, 165	0.73	0.571
Fertilization (FERT)	1, 165	0.78	0.377
GEN × FERT	1, 165	0.02	0.898
SPP × FERT	2, 165	3.89	0.022
GEN × SPP × FERT	2, 165	1.72	0.182
CON × FERT	2, 165	2.28	0.105
GEN × CON × FERT	2, 165	2.89	0.058
SPP × CON × FERT	4, 165	0.71	0.586
GEN × SPP × CON × FERT	4, 165	0.63	0.642
Variance component estimates			
Variance component	df	Estimate	SE
Pot (GEN × SPP)	33	0.0006	0.0004
Residual	165	0.0046	0.0005

Note: The model is a four-way factorial in a split-plot design. Data were arcsine square-root transformed prior to analysis.

Daughter ramets developed during early summer and fall. In early summer, the initiation of daughter ramets was not influenced by barrier species (Fig. 6, top right side). In fall, however, almost three times more daughter ramets emerged in bins of the winter annual *Bromus* than in bins of either of the two perennials (Fig. 6, bottom right side).

Clonal biomass

Total clonal biomass of *Elymus* plants was affected by the species of barrier plant, constraint environments, and fertilization (Fig. 7; Table 7, SPP × CON × FERT interaction). *Elymus* generally had the same biomass in *Agropyron* and *Bromus* bins and considerable more in *Pseudoroegneria* bins. In full-constraint environments in *Pseudoroegneria* bins, fertilization exceeded the control biomass by >70%. In *Bromus* bins, fertilization was effective only in minimal-constrain environments, yielding nearly a 90% increase in biomass. In *Agropyron* bins, *Elymus* biomass was not affected by fertilization. The constraint environments affected biomass only in fertilized *Bromus* bins where there was greater biomass in the minimal-constraint environment than in the full- and partial-constraint environments. Clonal biomass did not differ for the two genotypes (Table 7).

DISCUSSION

The rhizomatous *Elymus* employed a variety of morphological responses both apparently to forage for local nutrient patches and to penetrate and circumvent root systems of different barrier species. All *Elymus* plants were able to locate and respond to the nutrient patches. Thus, a short-duration nutrient patch was sufficient to induce clonal responses in *Elymus*, yet from a clonal foraging perspective this was exhibited primarily in first- and second-order rhizome branching. The presence of different neighbor root systems affected the speed, but not the direction of *Elymus* rhizome growth as had been expected. Growth was slowed in that proportionally more rhizomes had reached the zones most distant from the *Elymus* mother plants in the sections without barrier plants than in sections with barrier plants, but *Elymus* rhizomes both penetrated and circumvented the densest parts of the root systems of all barrier species. Most rhizomes that penetrated root systems likely would have resumed exploratory growth if the experiment had continued. As will be developed in this discussion, *Elymus* clonal growth did not correlate directly with the different root densities of barrier species; thus, other root system properties, e.g., nutrient and water uptake, root exudates, and others, were apparently more important in their influence on *Elymus* behavior. Furthermore, *Elymus* clonal behavior appeared to be more influenced by the presence of neighbors than by the availability of nutrient patches and there was hardly any noticeable difference in clonal response between the two genotypes.

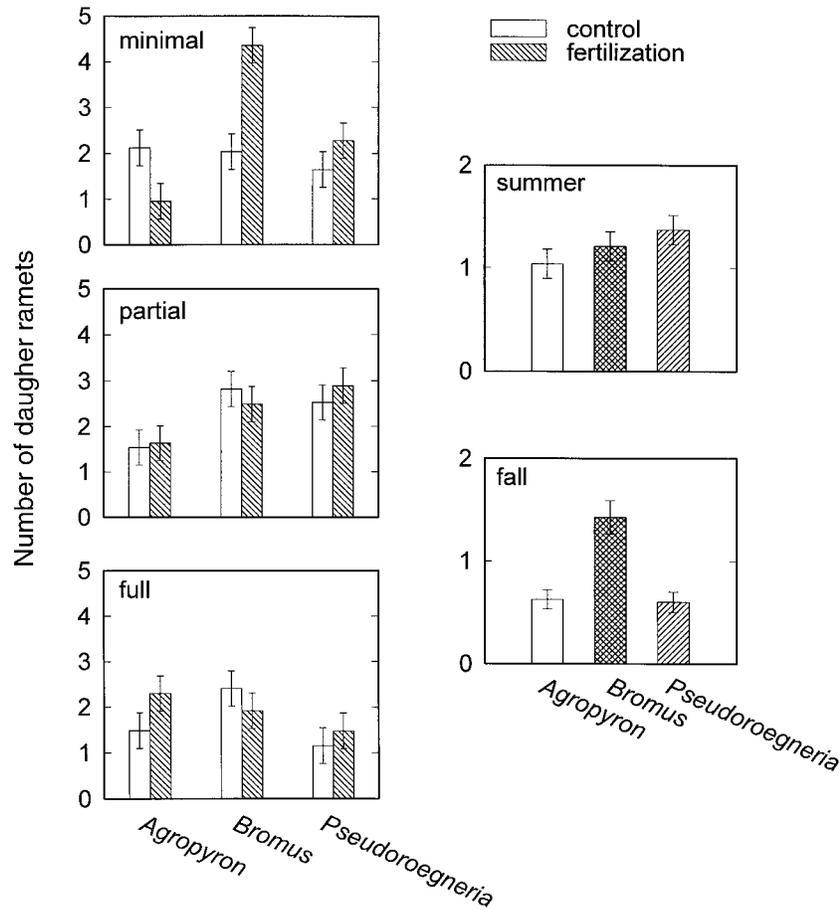


FIG. 6. Left side: Least-squares means (± 1 SE) of total number of daughter ramets of *Elymus* under fertilized (nutrient patch) and control (water patch) conditions in sections with minimal-, partial-, and full-constraint environments with the barrier species *Agropyron*, *Bromus*, and *Pseudoroegneria*. Right side: Least-squares means (± 1 SE) of average number of daughter ramets per section that emerged in summer and fall with different barrier species.

Effects of barrier species

Elymus exhibited several morphological changes that were markedly influenced by the species of barrier plant. The small size and linear structure of *Elymus* clones in the *Agropyron* bins indicated the presumably adverse neighborhood presented by this barrier species. In sections with *Agropyron* barrier plants, most of the rhizomes were not successful in penetrating the dense root systems, thus crossed over the top of the tussock crowns as stolons, or emerged as small daughter ramets. In *Bromus* bins, the influence of barrier plant root systems was limited to the time when this annual plant was active. Overall, *Elymus* produced shorter rhizomes with *Bromus* than with the two perennial barrier species, and rhizome branching was minimal. Much of the *Elymus* daughter ramet production occurred later in the season after *Bromus* had senesced. Thus, the growth barrier presented by *Bromus* may have been as severe as that presented by *Agropyron* in the early season, but ceased to be a major impediment by midsummer. *Elymus* biomass production and morphological responses

in *Pseudoroegneria* bins indicated a much more favorable environment than in the *Agropyron* and *Bromus* bins. *Elymus* produced many first- and second-order rhizomes in the *Pseudoroegneria* bins. *Elymus* rhizomes readily penetrated the densest portions of the tussock bases and produced large daughter plants in the midst of the *Pseudoroegneria* tussocks (data not shown).

As in our study, Schmid and Bazzaz (1992) found that initiation of rhizome branching in four rhizomatous species, *Aster lanceolatus* and three species of *Solidago*, was influenced more by the species of neighboring plants than by local soil fertility. In contrast with our study, rhizome branching in their species was more pronounced when growing with neighbor species with high root density than with low root density.

Elymus rhizomes branched prolifically, however, only on one or two first-order rhizomes regardless of the total number, length, or age of these first-order rhizomes in the same local environment. This suggests that ramets responded independently to local conditions and also that not all ramets encountering favor-

TABLE 6. ANOVA of total number of daughter ramets of *Elymus* examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
Genotype (GEN)	1, 33	14.72	0.001
Species (SPP)	2, 33	6.36	0.005
GEN × SPP	2, 33	0.28	0.760
Constraint (CON)	2, 165	2.08	0.128
GEN × CON	2, 165	1.75	0.177
SPP × CON	4, 165	3.89	0.005
GEN × SPP × CON	4, 165	0.74	0.567
Fertilization (FERT)	1, 165	0.70	0.406
GEN × FERT	1, 165	0.20	0.657
SPP × FERT	2, 165	1.11	0.333
GEN × SPP × FERT	2, 165	0.14	0.867
CON × FERT	2, 165	0.50	0.609
GEN × CON × FERT	2, 165	0.68	0.507
SPP × CON × FERT	4, 165	4.90	0.001
GEN × SPP × CON × FERT	4, 165	0.70	0.590

Variance component estimates			
Variance component	df	Estimate	SE
Pot (GEN × SPP)	33	0.0063	0.011
Residual	165	0.2136	0.023

Note: The model is a four-way factorial in a split-plot design. Data were log-transformed prior to analysis.

able conditions (i.e., nutrient patches) necessarily responded by increased branching in or near the patches as has been found in other work (but see Noble et al. 1979, Chapman 1983). The limited commitment to branching of the first-order rhizomes permits the remainder of the clone to continue searching for resources which should facilitate the exploration for other fertile sites (Slade and Hutchings 1987b, de Kroon and Schieving 1990). The evolutionary and ecological significance of such independent rhizome behavior in heterogeneous environments has been recently discussed (Turkington et al. 1991, Stuefer et al. 1996).

Effects of nutrient patches

The manner in which *Elymus* exhibited foraging behavior, i.e., modified its morphology in response to nutrient patches, varied with the different barrier species. For sections with *Agropyron* plants, *Elymus* appeared to forage for nutrients in that it increased daughter ramet production. Yet, in fertilized sections of the *Agropyron* bins without barrier plants, *Elymus* produced long rhizomes extending away from the mother plants, a response often interpreted as an indication of avoidance and escape from dense root systems of neighboring plants (Schmid 1985, Eriksson 1986). In minimal-constraint environments of *Bromus* bins, *Elymus* produced more daughter ramets if fertile soil patches were present. In the *Pseudoroegneria* bins, it was *Elymus* rhizome branching that was clearly promoted by the presence of fertile patches. This and a previous study (Humphrey and Pyke 1997) clearly indicate that *Elymus* clonal plasticity in effectively gar-

nering nutrients from locally enriched sites is not always expressed in a single trait or set of traits (i.e., increased rhizome branching, increased number of daughter ramets, and others). In situations with interacting plants, *Elymus* foraging response seems to be influenced by several factors simultaneously, e.g., type of species, root density, nutrient uptake capacity of neighboring plants, scale of nutrient heterogeneity, influence of root exudates, and other factors. This complicates the interpretation of specific plastic responses of *Elymus* in heterogeneous nutrient environments in natural settings. Longer term studies to examine the actual benefit of the different specific plastic responses of *Elymus* when growing with other common species of the sagebrush steppe would be useful.

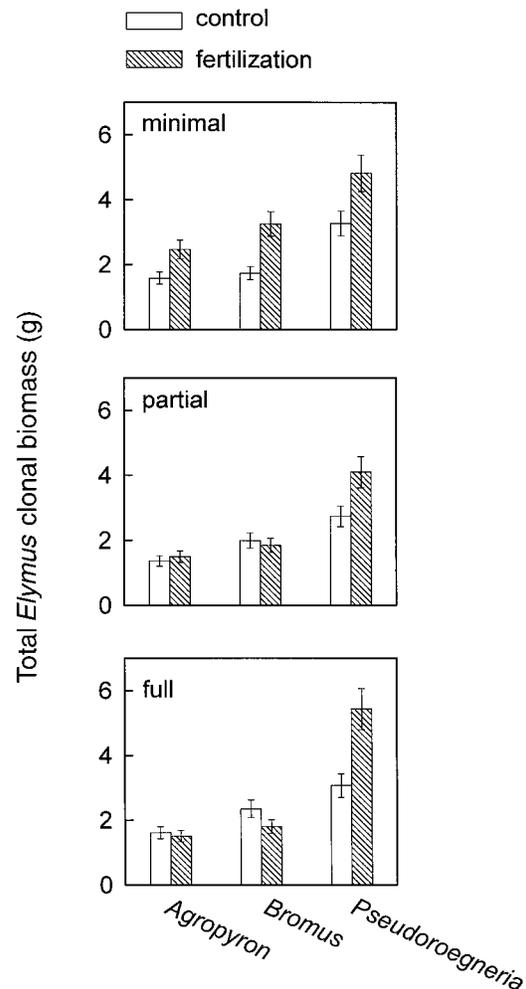


FIG. 7. Least-squares means (± 1 SE) (backtransformed from the log scale) of total clonal biomass (mother shoot, daughter shoot, rhizomes) for *Elymus* plants in control (water patch) and fertilization (nutrient patch) treatments in full-, partial-, and minimal-constraint environments for each of the three barrier species, *Agropyron*, *Bromus*, and *Pseudoroegneria*.

TABLE 7. ANOVA of total clonal biomass of *Elymus* examining the effects of genotype (GEN), barrier species (SPP), constraint environment (CON), and fertilization (FERT).

Tests of fixed effects			
Source of variation	df	F	P
Genotype (GEN)	1, 33	3.35	0.076
Species (SPP)	2, 33	43.05	0.001
GEN × SPP	2, 33	0.17	0.842
Constraint (CON)	2, 165	6.14	0.003
GEN × CON	2, 165	0.68	0.509
SPP × CON	4, 165	0.70	0.593
GEN × SPP × CON	4, 165	0.31	0.873
Fertilization (FERT)	1, 165	18.37	0.001
GEN × FERT	1, 165	1.30	0.256
SPP × FERT	2, 165	4.10	0.018
GEN × SPP × FERT	2, 165	0.41	0.667
CON × FERT	2, 165	5.38	0.006
GEN × CON × FERT	2, 165	0.63	0.536
SPP × CON × FERT	4, 165	2.87	0.025
GEN × SPP × CON × FERT	4, 165	0.66	0.621
Variance component estimates			
Variance component	df	Estimate	SE
Pot (GEN × SPP)	33	0.026	0.014
Residual	165	0.175	0.019

Note: The model is a four-way factorial in a split-plot design. Data were log-transformed prior to analysis.

Effects of decomposing *Bromus* roots

Bromus plants senesced late in June, and by harvest at the end of October most of its roots were decomposed. Nutrients released during decomposition should have become available to nearby *Elymus* plants. If *Elymus* had acquired only a fraction of these released resources, we would have expected an increase in *Elymus* clonal biomass at least as high as in *Pseudoroegneria* bins. We also would have expected *Elymus* clonal biomass to have been greater in full- and partial-constraint environments, since there was more *Bromus* root biomass and, thus potentially more nutrients available than in minimal-constraint environments. This was not the case in that *Elymus* biomass remained equally small in all of the constraint sections of the *Bromus* bins (cf. Fig. 7). Yet, by fall, *Elymus* had produced more daughter ramets and had overall shorter first-order rhizomes than in bins with the two perennial grasses, suggesting that *Elymus* probably foraged for some of the released nutrients in all sections of the *Bromus* bins. It seems surprising, however, that *Elymus* did not initiate first- and second-order rhizome branching as more nutrients became available. Thus, the *Elymus* clonal biomass and some morphology data in the *Bromus* bins do not indicate as strong a "nutrient release response" as would have been expected when roots decompose. This lack of response suggests that *Elymus* is either phenologically constrained, in that it is only able to garner nutrients from spring pulses (Bilbrough and Caldwell 1997), or that some factor was counteracting the positive response expected from *Elymus*. This may have

involved residues released by the decomposing *Bromus* roots.

Manifestations of interference

Competitive interactions in experiments are often assessed by plant biomass responses and sometimes by changes in morphological characteristics (Gaudet and Keddy 1988). There appeared to be pronounced differences in the effectiveness of the barrier species to interfere with *Elymus*. If root densities of barrier plants serve as an indicator of the potential for interference (Ennik and Baan Hofman 1983), *Elymus* should have produced more clonal biomass in sections without barrier plants (minimal constraint) than in sections with barrier plants (full or partial constraint) in the *Agropyron* bins. Yet, *Elymus* biomass was about the same in sections with high *Agropyron* root density as in minimal-constraint sections with low *Agropyron* root density. Overall, *Elymus* produced the greatest clonal biomass in sections with *Pseudoroegneria* barrier plants. There was some indication that nutrient competition might be involved in the case of *Bromus* as a barrier species. In minimal-constraint environments with low *Bromus* root density, *Elymus* produced more biomass with fertile soil patches than in controls. However, in sections with *Bromus* barrier plants, fertilization had no apparent effect on clonal biomass of *Elymus*. The biomass response of *Elymus* suggests that *Bromus* effectively reduced nutrient availability in sections with nutrient patches to levels similar to those in sections without nutrient patches.

If nutrient resource competition was primarily responsible for the *Elymus* clonal responses, one would expect *Elymus* to have exhibited similar behavior with all barrier species in minimal-constraint environments with nutrient patches. Since only a relatively small portion of barrier plant roots proliferated into minimal-constraint environments, root densities were similar among barrier species in these minimal-constraint sections (Fig. 2 bottom). Since *Pseudoroegneria* and *Agropyron* are strikingly similar in many root characteristics, such as root nutrient uptake capacity (Jackson et al. 1990, Caldwell et al. 1991), one can conclude that the two grasses would present similar potential resource competition in situations with the same rooting density. When additional nutrients were provided in minimal-constraint environments, there should have been similar, low levels of resource competition from the various barrier species. However, this was not the case; *Elymus* clonal responses depended very much on the species of barrier plant in the minimal-constraint sections. Thus, the few roots of the barrier species that entered minimal-constraint environments were sufficient to induce different responses by *Elymus*.

Another indication that simple resource competition does not explain *Elymus* success is the similar *Elymus* clonal biomass in all sections (constraint treatments) of both the *Agropyron* and *Pseudoroegneria* bins. This

seems surprising, since rooting densities were four and two to seven times greater in sections with than without barrier plants of these species. Yet, the very different rooting densities of these species did not translate into apparent differences in competitive outcome. On the other hand, the similar root densities in full-constraint environments of *Pseudoroegneria* bins and in the minimal-constraint environments of *Agropyron* bins (i.e., in the zone very near the barrier plant, where most barrier plant roots are likely to be found) caused very different *Elymus* clonal biomass and morphology. Thus, apparently other forms of interference were playing a more important role.

While our design did not allow us to separate nutrient competition from other forms of interference, these lines of evidence suggest that other forms of interference were important. These other forms of interference may include species-specific recognition and avoidance of neighboring plant roots (Mahall and Callaway 1991, Krannitz and Caldwell 1995, Huber-Sannwald et al. 1996, Mahall and Callaway 1996, Huber-Sannwald et al. 1997).

CONCLUSION

Clonal plasticity in the rhizomatous *Elymus* appeared to be functionally important both in foraging for favorable sites in these heterogeneous environments and in interacting with neighboring plant root systems. *Elymus* rhizomes penetrated, circumvented, and crossed over neighboring root systems. Differences in root densities and periods of active growth of neighboring plants did not result in the expected differences in *Elymus* morphological responses; instead these were influenced much more by other species-specific characteristics of the neighboring roots, which may have involved factors such as root exudates, residues of decomposing roots, or possibly mycorrhizal influences.

Foraging theory describes morphological responses of clonal plants to enhance the acquisition of spatially and temporally variable resources (de Kroon and Hutchings 1995). Several refinements and improvements of foraging theory have been proposed in the past few years (Herben et al. 1994, Hutchings and de Kroon 1994, Oborny 1994, de Kroon and Hutchings 1995, Cain et al. 1996, Newton and Hay 1996). Yet, foraging theory does not at this point adequately explain behavior in heterogeneous soil environments where both physical obstacles and neighboring root systems interfere with the exploration for patchy soil resources. Our study suggests that neighboring root systems greatly complicate rhizome behavior and intervene with both resource competition and other forms of interference.

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