Persistence of Idaho fescue on degraded sagebrush-steppe

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Abstract

Idaho fescue (*Festuca idahoensis* Elmer), a palatable native perennial bunchgrass, has persisted on degraded sagebrush-steppe despite invasion by alien plants, excessive livestock grazing, and increased density of woody vegetation due to fire suppression. Survival of these populations in the presence of competitive alien plants suggested 2 possibilities: 1) that Idaho fescue produces seedlings that successfully compete for soil resources with alien invaders, and 2) that Idaho fescue seedlings tolerate stress caused by resource uptake by alien neighbors. We compared germination and growth of Idaho fescue from an undisturbed population with that of conspecific populations from disturbed (grazed and invaded) sites to determine whether disturbed-site seedlings had greater potential for resource capture. Recruitment in Idaho fescue from degraded sites did not appear to be aided by rapid seed germination or greater tolerance of moisture stress during germination. A greater proportion of seeds from the undisturbed site germinated; they germinated faster, and were no more sensitive to water stress, than were seeds from disturbed sites. For both groups, decreasing water potential from 0 to –0.5 MPa had little effect on germination percentages but declined at –1 Mpa. Germination rates slowed with decreasing water potential. Though Idaho fescue from undisturbed and disturbed sites extended roots down the soil profile with equal speed, seedlings from the undisturbed site produced 3.5 times more root length, had 2.7 times greater root length density, and 3.4 times more leaf area than disturbed-site Idaho fescue. The higher growth rate and greater root length density in Idaho fescue from the undisturbed site translates to greater exploration and exploitation of the environment. The 2 Idaho fescue groups had equivalent specific root length, specific leaf area, and root weight ratio. Idaho fescue from disturbed sites showed strong, positive geotropic growth whereas branching and diageotropic growth were greater in Idaho fescue from the undisturbed site. Cheatgrass (*Bromus tectorum* L.) extended roots faster than did Idaho fescue, with 17 times the root length, 6 times the root length density, and 10.8 times the leaf area of undisturbed-site Idaho fescue. Cheatgrass and Idaho fescue had equivalent specific leaf area, but specific root length of Idaho fescue was nearly twice that of the alien. Roots accounted for about

Abstract

Idaho fescue (*Festuca idahoensis* Elmer), est une espèce locale, palatable, pèrrenne qui a persisté dans les steppes dégradées malgré l'invasion par d'autres espèces introduites, un surpaturage, et une densité croissante d'espèces ligneuses suite à la suppression des incendies. La survie de ces populations en présence d'une compétition avec les plantes introduites est expliquée par deux facteurs possibles: 1) Idaho fescue est capable de produire des jeunes plantes qui concurrent avec succés en matière de ressources édaphiques avec les autres espèces introduites, et 2) les jeunes plantes d'Idaho fescue peuvent supporter des périodes de stress manifestées par le manque de ressources causé par les espèces voisines introduites. Nous avons comparé la germination et le développement d'Idaho fescue une population non-perturbée avec une population provenant de sites perturbés (surpaturés et envahis), et ce pour déterminer si les jeunes plantes dans les sites perturbés ont un potentiel plus important pour capturer le maximun de ressources. Dans les sites perturbés le recrutement d'Idaho fescue ná pas semble pas été favorisé par une germination rapide des semences ou par une plus grande tolérance au manque d'eau durant la germination. Le taux de germination de semences proveane de sites non perturbés a été supérieur, ils ont germiné plus rapidement, et ils ont été moins sensible au stresss hydrique, par rapport aux semences de sites perturbés. Pour les deux groupes, la diminution du potentiel hydrique de 0 à 0,5 MPa avait un faible impact sur le taux de germination, mais ce dernier est alteré à -1 MPa. Le taux de germination se ralentis avec la diminution du potentiel hydrique. Bien que la vitesse a été la même pour les deux groupes, dans les sites non perturbés, les jeunes plantes ont produit des racines 3,5 fois plus long, ayant une densité 2,7 fois plus grande, et un feuillage 3,4 fois plus important que les jeunes plantes d'Idaho fescue des sites perturbes. La supériorité du taux de croissance ainsi que la densité des racines d'Idaho fescue des sites non perturbés ont revèlet une plus grande exploration et exploitation de l'environnement. Les deux groupes d'Idaho fescue ont eu la même longueur de racines specifiques, la même surface de feuillage, et le même ratio du poids des racines. Idaho fescue des sites perturbés a demontré une forte et positive croissance <u>géotropique</u>, alors que le branchage et la croissance <u>diageotropique</u> ont été plus important dans les sites non perturbés. Cheatgrass (*Bromus tectorum* L.) à des racines se propageant beaucoup plus vite qu'Idaho fescue, ayant une longueur 17 fois plus grande, une densité 6 fois plus importante et une surface des feuilles 10,8 fois supérieure par rapport à Idaho fescue des sites perturbés. Cheatgrass et Idaho fescue ont eu une surface des feuilles équivalentes, mais la lonqueur specifique desracines d'Idaho fascue a été deux fois plus

31% and 55% of cheatgrass biomass. Competitive ability did not appear to promote recruitment in Idaho fescue populations on degraded rangelands. Idaho fescue seedlings from the undisturbed-site were better competitors than disturbed-site seedlings, but interference from neighboring cheatgrass most strongly inhibited shoot growth of both Idaho fescue and cheatgrass. Idaho fescue had little effect on cheatgrass shoot growth. Selection of stress-tolerant genotypes from original populations may best explain the continued existence of Idaho fescue on grazed and invaded sites. We suggest that tolerance of moisture stress combined with vegetative longevity, are mechanisms behind Idaho fescue's persistence.

importante que celle de l'espèce introduite. Le rapport des racines á la biomasse était de 31% et 55% respectivement pour Idaho fescue et Cheatgrass. L'habilité compétitive d'Idaho fescue ná pas semblé favoriser le recrutement de nouvelles populations dans les parcours dégradés. Les jeunes plantes d'Idaho fescue des sites non-perturbés ont été plus compétitifs que celles des sites perturbés, mais d'avoisinoge le du Cheatgrass a inhibé fortement la croissance des ie unes pousses d'Idaho fescue ainsi du Cheatgrass. L'impact d'Idaho fescue sur la croissance des pousses chez le Cheatgrass a été faible. La sélection de génotype tolérant le stress à partir des populations originales (locales) pourrait mieux expliquer la persistence d'Idaho fescue dans les sites surpaturés et envahis. Nous suggérons qu'il y à des mécanismes de tolérance du stress hydrique en combinaison avec la longévité végétative sont à la base de la persistence d'Idaho fescue.

Key Words: ecotype, seed germination, seedling growth, demography, restoration, invasion, *Bromus tectorum*

In sagebrush-steppe, plant growth is most limited by available soil moisture (Smith and Nowak 1990, Ries and Fisser 1979). Precipitation falls primarily during winter, and growth of sagebrush-steppe bunchgrasses depends largely on stored soil moisture (Cline et al. 1977). Rapid exploitation of soil moisture is a measure of competitiveness in this system (Eissenstat and Caldwell 1988). With early, extensive, and rapid root growth, the alien winter annual cheatgrass (*Bromus tectorum* L.) is an effective competitor for moisture (Melgoza et al. 1990, Mack 1981, Cline et al. 1977, Harris 1967, Robertson and Pearse 1945).

Idaho fescue (*Festuca idahoensis* Elmer), a native perennial bunchgrass, persists on degraded central Oregon sagebrush-steppe despite invasion by cheatgrass (Mack 1981), increased tree and shrub density from fire suppression (Miller and Wigand 1994, Burkhardt and Tisdale 1976), and overgrazing by livestock since the late 1800's (Galbraith and Anderson 1971, Strong 1940). Long-term grazing and alien invasion have extirpated some populations of Idaho fescue from similar sites in central Oregon (Driscoll 1964). Persistence of Idaho fescue on degraded sites may be explained by ecotypic differentiation, because introductions of cheatgrass and domestic livestock changed selective pressures

affecting native bunchgrasses (Mack and Thompson 1982, Mack 1981). Neither heavy grazing nor alien invasion has driven these populations to extinction, suggesting adaptation to new selective pressures (Knapp and Rice 1994). Persisting populations may offer potential for restoring Idaho fescue to sites from which it has been eliminated.

Plausible explanations for persistence of Idaho fescue on degraded sites include: persisting populations are composed of the most competitive, or alternatively the most stress-tolerant, genotypes of the original populations; persisting plants are less palatable; or persisting plants better tolerate defoliation. This study tested the hypothesis of greater competitive ability in disturbed-site Idaho fescue. A test of the defoliation tolerance hypothesis is found in Jandl et al. (1994, see discussion below). The stress tolerance and palatability hypotheses remain untested, although our observations that are pertinent to these hypotheses are discussed.

We assayed competitive abilities of Idaho fescue seedlings from populations persisting on grazed and invaded (disturbed) sites and an ungrazed (undisturbed) relict site with little cheatgrass. Recruitment into persisting populations requires the Idaho fescue

seedlings compete with co-occurring species for soil resources (see Buman et al. 1988). We used cheatgrass as our model competitor because it is an aggressive, pervasive alien grass. Germination of ruderal species like cheatgrass is often relatively insensitive to water stress (Evans and Etherington 1990, Thill et al. 1979). Among neighboring seedlings, emergence increases resource capture although at the risk of freezing damage (Weiner 1985, Mack and Pyke 1983). Therefore, we predicted that proportinately more Idaho fescue seeds from disturbed sites would germinate and they would germinate more rapidly than seeds from the undisturbed population of Idaho fescue, and that germination of disturbed-site Idaho fescue seeds would be less sensitive to moisture stress. To compete with cheatgrass for soil moisture, Idaho fescue seedlings would have to extend roots into soil at rates comparable to cheatgrass. Otherwise, Idaho fescue roots would be left in soil from which cheatgrass had removed stored moisture (Melgoza et al. 1990, Reichenberger and Pyke 1990, Harris 1967). Accordingly, we predicted that Idaho fescue persisting on disturbed sites would have greater root and shoot growth rates, specific root length, and specific leaf area compared to seedlings from the relict population, and that growth rates and root extension rates of disturbed-site Idaho fescue would be comparable to those of cheatgrass. Lastly we measured shoot biomass of Idaho fesuce and cheatgrass seedlings grown in monoculture and mixture to measure competitive abilities. We predicted that disturbed-site Idaho fescue would inhibit cheatgrass growth more strongly than Idaho fescue from the undistrubed site.

Methods

Materials

Seeds of Idaho fescue and cheatgrass were harvested in July, 1989, at 5 sites in central Oregon selected for their similarity (Fig. 1). Site descriptions are summarized in Tables 1 and
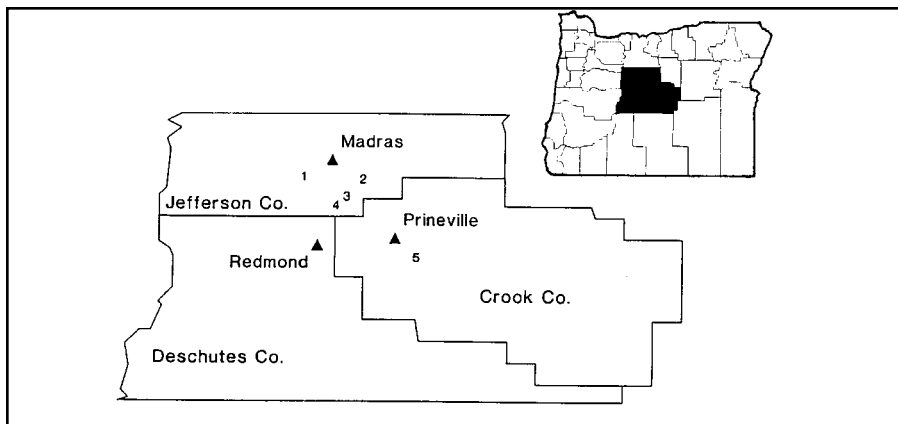
Fig. 1. Locations of climate stations and seed collection sites in central Oregon: 1 Island, 2 Blanchard, 3 Lone Pine, 4 McCoin, 5 Combs Flat. The distance between sites 1 and 5 is roughly 50 km.

2 and Figure 2. Precipitaiton in 1989 was above normal and seeds were abundant. Collected seeds were mechanically threshed and a seed blower was used to sort filled seeds from chaff and unfilled seeds. The blower setting was constant for all conspecific seed lots and mean seed mass within a species did not differ following cleaning. Seeds were stored in paper bags at room temperature following processing. Our experiments were run in 1991.

Given the history of livestock production in central Oregon (Galbraith and Anderson 1971, Strong 1940) and the palatability of Idaho fescue (Vavra

and Sneva 1978, Dragt and Havstad 1987), all sites except the relict area have very likely been grazed by domestic livestock for 125 years. The relict Idaho fescue population grows on the Island, a plateau rimmed with 5–70 m basalt cliffs. Difficult access and lack of water have largely precluded livestock grazing. As far as is known, the Island has been grazed only by sheep for 2 successive summers during the 1920s (Driscoll 1964). Cheatgrass density is low on the Island compared to our other sites (Table 2). We considered the Island an undisturbed site.

Seed Germination Experiment

Our predictions were: 1) Idaho fescue seeds from disturbed sites germinate in higher amounts and faster rates than seeds from the undisturbed site; and 2) germination is more strongly inhibited by increasing water stress in seeds from undisturbed sites than those from the disturbed site.

We tested germination of Idaho fescue seeds in 3 completely randomized experiments to test the above 2 predictions under different environmental conditions. Each experiment used a programmable germinator to simulate a regime of temperature and photoperiod typical of central Oregon during August, September, and October:

August 8°C(6 hrs)/29°C (18 hrs); 14 hrs light

September 4°C(7 hrs)/23°C (17hrs); 12 1/2 hrs light

October 1°C (hrs)/18°(16 hrs); 11 hrs light

Temperatures selected are mean minimum and maximum of the months (Anon. 1983, 1981–1989), and each is based on data from climate stations surrounding the seed collection sites (Prineville, Redmond, and Madras, Ore., Fig. 1). Mean maximum and minimum temperatures were used because temperature fluctuations at the soil surface are greater than those measured in macroclimate data (Ehleringer 1985), and we lacked soil

Table 1. Topographic and edaphic properties of the seed collection sites in Oregon.

	Elev.	Slope & Aspect	Soil Series	Soil Classification	Effective Rooting Depth[1]	Available Water Holding Capacity[2]	pH	Surface Horizon (0–5 cm) P	NH$_4$-N	NO$_3$-N
	(m)				(cm)	(cm)		------ (mg/kg) ------		
Island	740	plateau	Agency-Madras complex[3]	Xerollic Camborthid & Xerollic Duragrid	69–84	7.6–10.2	6.6	22.5[4]	4.03	1.74
McCoin	1015	35%, N	Prag	Pachic Palexeroll	56–102	7.6–15.2	6.6	17.5	4.56	1.71
Blanchard	1185	5%, N	Gribble	Argic Durixeroll	76–94	5.1–12.7	6.8	19.5	3.78	0.55
Lone Pine	970	40%, NW	Currant-Tub mix	Calcic Pachic Haploxeroll & Calcic Pachic Argixeroll	76–152	7.6–30.5	6.9	20.0	3.57	0.64
Combs Flat	1050	20%, N	Lookout	Argic Durixeroll	45–76	6.1–7.0	6.8	22.5	3.76	0.53

[1]Depth (cm) to an indurated layer or unweathered bedrock.
[2]Available water holding capacity (cm) of entire profile to effective rooting depth.
[3]Preliminary USDA NRCS survey and classification.
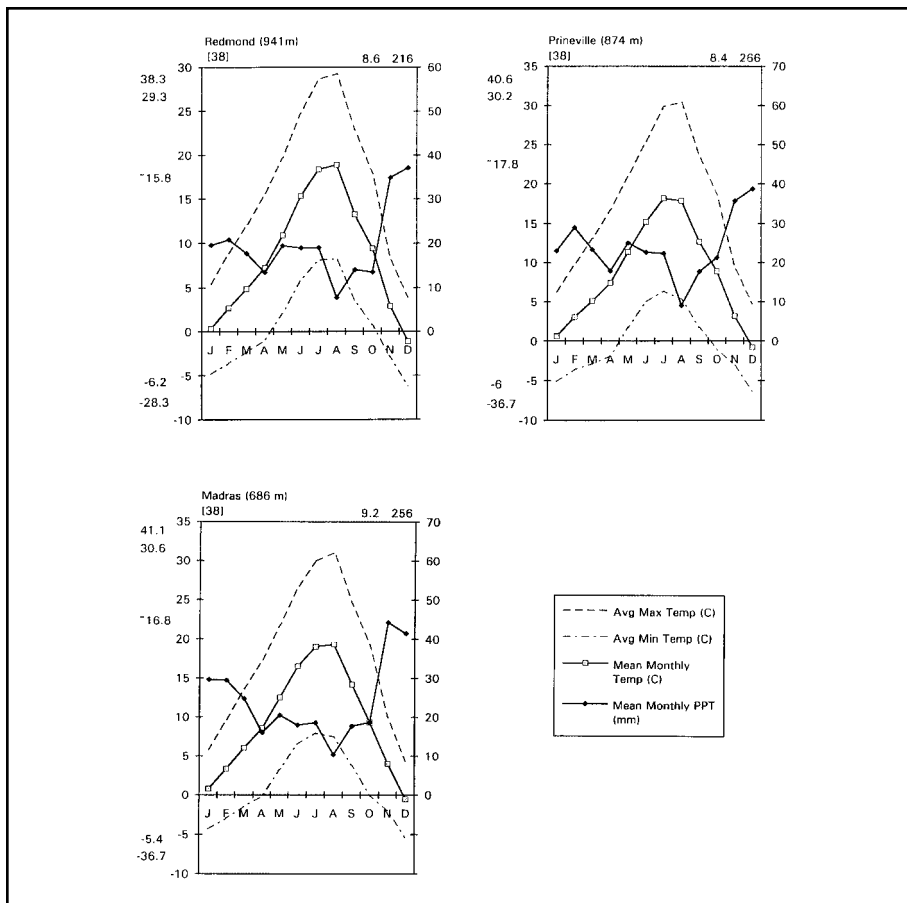[4]Nutrient concentrations in mg/Kg.

Fig. 2. Climate diagrams for Redmond, Prineville, and Madras, Ore. (Walter 1985). The station's name and elevation are followed in the next row by the number of years of data compiled for the diagram (in brackets), and mean annual temperature (°C) and precipitation (mm). The right axis is precipitatipn; the left axis is temperature. The numbers to the left of the left axis are, from top to bottom, highest temperature recorded, mean daily maximum temperature for the warmest month, mean diurnal temperature fluctuation, mean daily minimum temperature for the coldest month, and lowest temperature recorded.

surface temperatures. Temperature duration is based on hourly air temperatures (1986–1988) recorded at Redmond. Photoperiod was taken as mid-month day length in the study area (44° 21'N, 120°54'W). Lights were on during the warm period, but because the warm period exceeded the lighted period, seeds were exposed to cold + dark, warm + dark, and warm + lighted conditions.

Within each experiment, we simulated wet, intermediate, and dry months using 3 levels of water potential: distilled water (osmotic potential 0 MPa) or polyethylene glycol (PEG) solutions having osmotic potentials of –0.5 and –1.0 MPa (Michel 1983, Equation 1). Potential of a PEG solution varies with temperature, so solutions were prepared to give desired potential dur-

ing the warm period. Fungicides were not employed because addition of fungicide would have altered the solution's osmotic potential to an unknown value (Michel 1983). A germination substrate can alter the potential of a PEG solution by taking up water but not larger PEG molecules, so the ratio of solution (ml) to substrate mass (g) should be 12 or greater (Hardegree and Emmerich 1990); our ratio was 14.3 (50 ml/3.5 g).

We germinated seeds on cellulose in transparent boxes; all seeds were in contact with saturated substrate. Boxes were sealed in transparent plastic bags to maintain high humidity. Fifty seeds in a germination box constituted an experimental unit. Treatments were randomly assigned to experimental units and replicates (4)

were randomly assigned to 1 of 10 shelves in a germinator, with only 1 replicate of any treatment per shelf. August and September experiments were run concurrently in separate germinators. After the August and September experiments, 1 germinator was reprogrammed to simulate October conditions. We defined germinations as elongation of a seminal root or coleoptile to 5 mm. Boxes were examined for germinated seeds daily and germinated seeds were removed. Each germination trial ran for 30 days unless, once seeds began germinating, 1 week passed with no additional germination. From germination data we calculated percent germination, days to start of germination, median response time, and Maguire's (1962) coefficient of the rate of germination (CRG). The time required for 50% of seeds that actually germinated in each replicate to germinate equaled median response time. The CRG values were calculated as:

$$CRG = \sum_{i=1}^{30} \left[\frac{N_i}{T_i} \right] \qquad (1)$$

where N_1 is the number of seeds germinating on the ith day and T_i is the ith day from sowing.

We used Number Cruncher Statistical System (NCSS, Hintze 1990) in our analyses. Response variables (percent germination, days to germination, median response time, and CRG) passed normality, outlier, and variance tests. Therefore, we analyzed untransformed data using 2-factor (population and water potential) ANOVA with contrasts to test hypothesized differences. We separated means, where appropriate, using Fisher's LSD ($\alpha = 0.05$).

Growth and Allocation Experiment

We examined root and shoot growth in Idaho fescue seedlings from undisturbed and disturbed sites and cheatgrass seedlings. Seedlings were grown in a greenhouse in a double tube assembly: a soil-filled glass root tube (51 mm $\times$ 122 cm) and a black plastic pipe of slightly larger diameter which protected the root tube from breakage and excluded light. Root tubes slid out

Table 2. Vegetation[1] at the seed collection sites in July 1992.										
	Idaho fescue		cheatgrass		bluebunch wheatgrass		sagebrush		western juniper	
	canopy cover	denstiy	canopy cover	density	canopy cover	density	canopy cover	density	canopy cover	density
	(%)	(#m^{-2})	(%)	(#m^{-2})	(%)	(#m^{-2})	(%)	(#m^{-2})	(%)	(#m^{-2})
Island	6	3.6	—[2]	—	6	4.0	2	0.4	—[2]	—
McCoin	8	6.4	<1	6.0	2	3.2	—[2]	—	41	0.4
Blanchard	7	6.4	11	254.0	3	11.6	<1	0.8	7	0.8
Lone Pine	2	3.2	<1	11.2	<1	1.2	—[2]	—	28	0.8
Combs Flat	<1	0.4	9	254.4	<1	1.2	5	0.4	19	0.8

[1]Seed Goodwin (1993) for community composition data for each site.
[2]Present at site but did not appear in the 0.25 m2 sample plots (n = 10).

of protective tubes for observation. Tube assemblies were inclined to allow nondestructive root measurements. A root tube containing an individual seedling constituted an experimental unit. For repeatedly measured variables, the experimental unit for treatment was a seedling, and the experiment unit for time was a 1 week interval within a seedling. We used a completely randomized design with 5 replicates. Treatments were randomly assigned to experimental units, and root tubes were randomly assigned to positions in the supporting frame.

We filled root tubes with soil from Combs Flat in an effort to duplicate an indigenous soil profile. A 1.2 m pit was dug and excavated soil separated by strata; soil from the lowest stratum was added to root tubes first and surface soil was added last. Soil was not amended or sterilized. Soil was brought to field capacity 2 weeks before seeds were planted and indigenous seedlings removed. Tap water (about 50 ml) was added to tubes at the time of planting, with subsequent watering as needed to prevent wilting. Cheatgrass germinates more rapidly than Idaho fescue (Doescher et al. 1985, Thill et al. 1979), so cheatgrass was planted 4 days after Idaho fescue to synchrozine emergence. Because time of emergence varied among seedlings, harvest dates were adjusted to allow an equal period of growth for all seedlings.

Seedlings were grown with alternating day/night temperatures of 24° and 18°C. Ambient Jaunary daylight was supplemented by florescent tubes giving a PPFD of 206 µmol m^{-2} sec^{-1}.

Lights were on for 14 hours/day. Temperatures in glass root tubes were monitored at depths of 5, 15, 25, 50, 75, and 100 cm. Root tube temperature declined with depth, from 23°C at 5 cm to 16°C at 100 cm. Rooting depth, shoot height, and number of leaves were recorded weekly. Rooting depth equaled distance from germinated seed to lowest root tip. Because internodal elongation is limited to reproductive culms in Idaho fescue, shoot height was measured as vertical distance from soil surface to tip of the longest leaf held vertically. After 60 days, seedlings were harvested. Ten fully-expanded leaf blades were collected to determine mean leaf area; all leaves were used when fewer than 10 had been produced. Leaf area was calculated as surface area of a cone for Idaho fescue (filiform, rolled blades) and area of a triangle for cheatgrass (flat blades). Total plant leaf area was calculated by multiplying mean leaf area by number of leaves.

Roots were separated from saturated soil by sliding a soil column onto a screen immersed in water, allowing harvest of an intact root system in most cases. Extracted root systems were cleaned and, after drying at room temperature for 30 minutes, weighed. Roots were partitioned by soil stratum (0–2, 2–5, 5–10, 10–20, 20–50, 50–120 cm). Three root samples were randomly selected from each stratum and length and mass measured. In some cases, particularly at depths of greatest penetration, only 1 or 2 root segments were available. The length of a root segment was determined by measuring the length of the primary

root axis and then adding the visually-estimated length of fine laterals. Total root length was calculated from mean length per unit mass of samples. Harvested root length, root length density, and ratios of root weight:plant weight and root length:leaf area were calculated.

Data were analyzed using 1-way ANOVA (seedling emergence, total root length, root length density, root mass, leaf area, specific leaf area, shoot mass, and root weight:plant weight and root length:leaf area ratios), 2-way ANOVA (root biomass distribution in the soil column), and repeated measures ANOVA (rooting depth, leaf length, and number of leaves). NCSS (Hintze 1990, 1992) was used for 1- and 2-way ANOVA, and Statistical Analysis System (SAS 1987) for repeated measures ANOVA. Because of missing observations, data from week 1 were excluded from analyses of rooting depth and shoot height. Additionally, a replicate seedling in 2 of 5 *Festuca* populations died prior to completion of the experiment; data for these seedlings were excluded.

For each population, data were tested for conformance to ANOVA assumptions. Logarithmic (base e) transformations were required for rooting depth, total root length, root length density, and number of leaves. Repeatedly-measured variables failed tests of sphericity, so multivariate tests were used for the subplot factor (time) and the interaction of time and treatment. Differences between undisturbed and disturbed Idaho fescue populations were tested using con-

trasts. To allow comparison with cheatgrass when a tranformation was required, untransformed means are reported with differences determined using log tranformed data. Means for cheatgrass were many times greater than those of any Idaho fescue population in many cases, and differences among Idaho fescue populations could not be detected when cheatgrass was included in the analysis. Because variation within Idaho fescue was the focus of this research, cheatgrass was excluded from these analyses.

Replacement Series Experiment

We used a replacement series experiment to assess competitive abilities of seedlings of Idaho fescue grown with cheatgrass. In the replacement series, total density (283 plants m^{-2}) and spatial arrangement were held constant while the density of each species varied between 0 and 283 plants m^{-2} (proportions of 0IF:5C, 1IF:4C, 2IF:3C, 3IF:2C, 4IF:1C, and 5IF:0C). Monocultures of each species were also planted at densities above and below (509 and 57 plants m^{-2}) that used in the replacement series (Jolliffee et al. 1984) with spatial arrangement again constant within each density.

The experiment was run in a greenhouse using a randomized, blocked design. Each complete replacement series, plus additional monocultures, was randomly assigned to a location within a block. Treatments were replicated 4 times. Diurnal temperatures were 24° and 18°C, and ambient summer sunlight was not supplemented. Treatments consisted of 5 populations of Idaho fescue and cheatgrass: Combs Flat, Lone Pine, Blanchard, McCoin, and Island. Seeds from the same location were used when the 2 species were grown in mixture (e.g. McCoin Idaho fescue+ McCoin cheatgrass). Competitiveness of cheatgrass should not vary among populations given its low genetic diversity (Novak et al. 1991).

Plants were grown in 2,832 cm^3 pots filled with soil from Combs Flat. Two weeks prior to applying treatments, pots were watered to field capacity and indigenous seedlings removed. In mixtures, each species was randomly assigned to positions. Multiple seeds were planted at each position and thinned after emergence to 1 seedling. Cheatgrass seeds were planted 5 days after Idaho fescue to synchronize emergence. Pots were watered to field capacity 3 days before sowing seeds and were lightly watered at planting. Thereafter, pots were lightly watered twice a week. An aphid infestation occurred midway through the experiment, and greenhouse staff applied insecticidal soap, sulphur, sulpur and nicotine to all plants. Sixty days after planting, shoots were harvested, dried, and weighed.

Competitive ability was assessed through reciprocal yield analysis (Spitters 1983). Appropriate equations for a 2 species mixture are:

$$1/W_i = \beta_{0,1} + \beta_{1,i}N_i + \beta_{2,i}N_j + \quad (2)$$

$$1/W_j = \beta_{0,j} + \beta_{1,j}N_i + \beta_{2,j}N_i + \quad (3)$$

where W= dry biomass (g) and N = density (plants m^{-2}). The first subscripts denote βs 0, 1, and 2. The y-intercept (β_0) is the reciprocal of theoretical maximum biomass of a seedling grown under the experimental conditions but without interference, and β_1 and β_2 quantify intra- and interspecific competition, respectively. The 2 species of the mixture are identified by subscripts i and j. Relative competitive ability (RC) of a species is determined by $\beta_{1,i}/\beta_{2,i}$.

Data were fit to Spitters' (1983) model using NCSS (Hintze 1990). Weights were iteratively assigned and adjusted using robust regression until regression coefficients and absolute values of residuals stabilized. Within each treatment, some observations were assigned a weight of zero (discarded). Once weights had been assigned, weighted multiple regressions were run. Biomass data from both mixtures and monocultures were used to estimate regression coefficients, but seedlings that died during the experiment were excluded. Data from the 4 disturbed-site populations were pooled to test differences between these populations and the undisturbed population.

Results

Seed Germination Experiment

A greater proportion of Idaho fescue seeds from the undisturbed site germinated and did so at a greater rate than did seeds from disturbed sites (Table 3). Consequently germination coefficient (CRGs) of seeds from the undisturbed site were greater than those of disturbed-site seeds. Germination began earlier in seeds from the undisturbed site than in disturbed-site seeds under August conditions, but there were no differences in days to germination in the September and October experiments. Percent germination was highest under September and October conditions for both groups of Idaho fescue seeds; fewer seeds germinated under warmer August conditions. Seeds germinated most rapidly under September temperatures and most slowly in the cooler October experiment. Both Idaho fescue seed groups attained their highest CRGs in the September experiment.

Seeds from both Idaho fescue groups were strongly affected by changes in water potential (Table 4). Decreasing water potential delayed both initiation and rate of germination (Fig. 3). Reducing water potential from 0 to –0.5 MPa roughly doubled median response times, and they were almost tripled at –1 MPa. Water potential had less effect on percent germination, as the numbers of seeds germinating at 0 and –0.5 MPa were nearly equivalent. At –1 MPa, percent germination was reduced. Increasing water stress reduced CRGs. In the September experiment, CRG dropped from 6.77 at 0 MPa to 4.09 and 2.32 at –0.5 and –1 MPa respectively (standard error = 0.09). The effect of water potential on CRG varied with seed population in the August and October experiments. In both experiments, CRGs declined with decreasing water potential, and the trend was more distinct in disturbed-site seeds than in seeds from the undisturbed sites.

Growth and Allocation Experiment

Idaho fescue from the undisturbed site emerged 4 days earlier than seedlings from disturbed-site Idaho

Table 3. Germination responses under simulated autumn conditions of Idaho fescue seeds collected from populations on disturbed and undisturbed sites.				
	Undisturbed		Disturbed	
	Mean	SE	Mean	SE
August				
Germination (%)	74.95a	2.13	66.96b	1.07
Days to Germination	7.17a	0.40	8.33b	0.20
Median Response Time	12.50a	0.45	14.42b	0.23
GRG[3]	3.42a	0.11	2.76b	0.05
September				
Germination (%)	87.84a	1.77	83.58b	0.88
Days to Germination	5.75a	0.31	6.42a	0.16
Median Response Time	10.17a	0.40	11.46b	0.20
CRG	5.02a	0.11	4.24b	0.06
October				
Germination (%)	86.30a	1.64	82.18b	0.82
Days to Germination	8.83a	0.26	9.25a	0.13
Median Response Time	14.08a	0.29	14.95b	0.15
CRG	3.71a	0.08	3.18b	0.04

Within a row, different letters indicate significant differences ($\alpha = 0.05$)
[1]n = 12
[2]n = 48
[3]CRG equals Maguire's (1962) Coefficient of the Rate of Germination.

fescue populations (Table 5). Cheatgrass seedlings emerged 2.2 days sooner than Idaho fescue from the undisturbed sites. Undisturbed-site seedlings grew taller than disturbed-site seedlings, but the difference in rooting depth was only marginally significant (shoot height: $F = 6.79$, $p = 0.02$, rooting depth; $F = 3.41$, $p = 0.08$). Undisturbed-site seedlings had a shoot height of 13.1 cm after 8 weeks growth compared to 9.2 cm for disturbed-site Idaho fescue (Fig. 4). Idaho fescue seedlings extended roots to a depth of 35.5 cm. Cheatgrass grew faster than Idaho fescue, extending roots to 120 cm and shoots to greater than 30 cm. Idaho fescue from the undisturbed site had more leaves than seedlings from disturbed-sites ($F = 4.28$, $p = 0.05$), but cheatgrass produced leaves faster than either Idaho fescue group (Fig. 5). Total root length was roughly 3 times greater in undisturbed-site seedlings compared to disturbed-site seedlings; the same pattern was evident in leaf area (Table 5). Undisturbed-site seedlings had twice the root length density of disturbed-site seedlings. However, the 2 Idaho fescue groups had equivalent specific root length and specific leaf area. Cheatgrass averaged more than 10 times the root length and leaf area of undisturbed-site Idaho fescue, and root length density of the alien was 6-fold greater (Table 5). Cheatgrass had a specific root length half that of Idaho fescue, although the 2 species had equivalent specific leaf area. Both root and shoot biomass were greater in undisturbed-site Idaho fescue than in conspecifics from disturbed sites, but allocation patterns did not differ (Table 5). Roots accounted for roughly 31% of plant biomass in Idaho fescue. Cheatgrass biomass was much greater than that of Idaho fescue, with 55% belowground. The root length:leaf area ratio of cheatgrass was double that of Idaho fescue.

The distribution of Idaho fescue root biomass in soil varied with the interaction of population and soil strata ($F = 3.09$, $p = 0.01$). Seedlings from the undisturbed site concentrated roots in the upper strata of the soil profile, and had greater root biomass at all strata than disturbed-site seedlings (Table 6). Undisturbed-site seedlings had 65% of their root biomass in the upper 10 cm of the soil column, compared to 59% for disturbed-site seedlings. Cheatgrass rooted more deeply than Idaho fescue, with 40% of cheatgrass root biomass at 0 to 10 cm (Table 6). Cheatgrass root biomass was much greater than that of Idaho fescue at all depths, and cheatgrass root biomass did not consistently decline with increasing depth.

Replacement Series Experiment

Density of neighboring cheatgrass seedlings strongly affected shoot growth of both Idaho fescue and cheatgrass (Table 7). Undisturbed-site
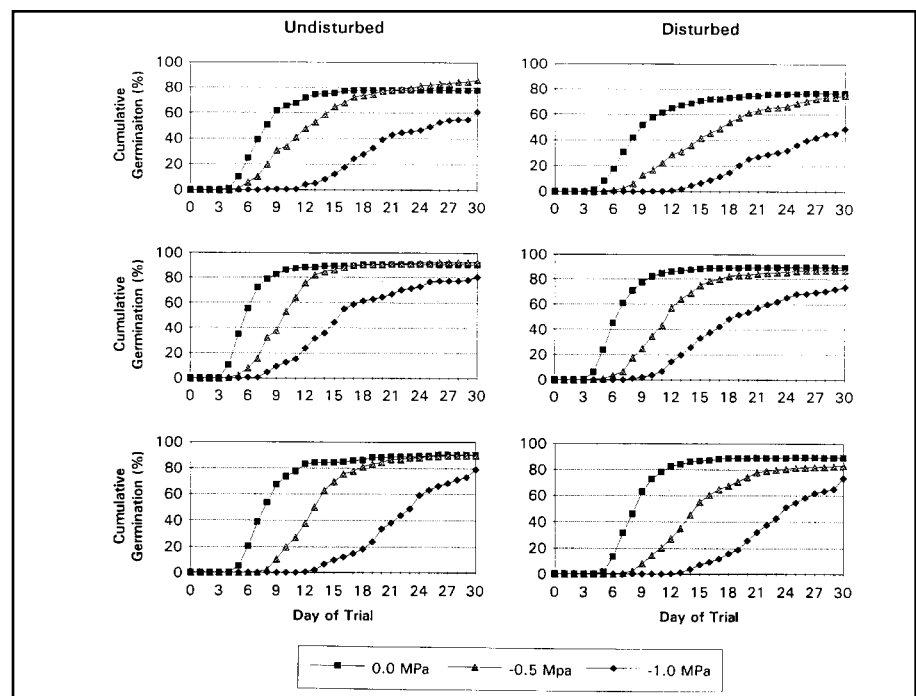

Fig. 3. Cumulative percent germination in Idaho fescue seeds from undisturbed and disturbed site populations in the August (top), September (middle), and October (bottom) experiments.
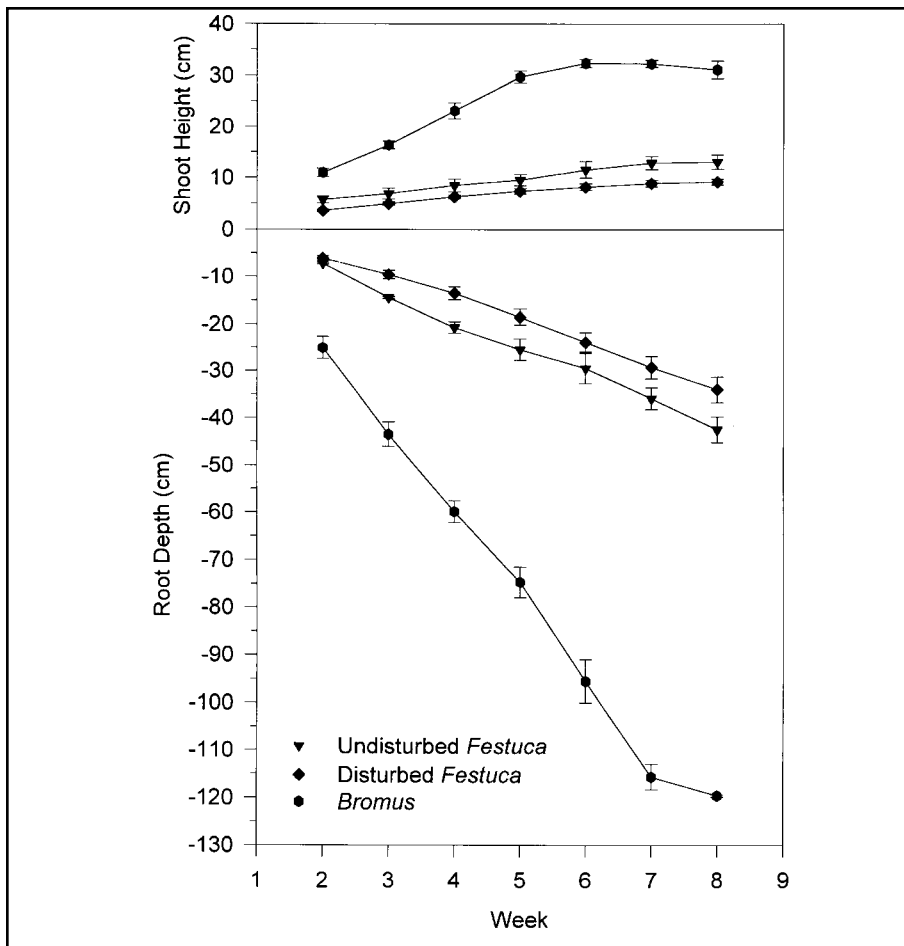
Fig. 4. Root and shoot growth by Idaho fescue from undisturbed and disturbed sites and by Bromus tectorum. Plots show untransformed means and associated standard errors to allow comparison of the 2 species; repeated measures analysis of log (e) transformed root depth data did not reveal a statistically significant difference ($\alpha = 0.05$) between the 2 Idaho fescue groups.

Idaho fescue seedlings were better competitors than conspecifics from disturbed sites, but interference from Idaho fescue had little influence on shoot growth by either species. Equations for seedlings from the undisturbed site were both highly significant (Idaho fescue; $F = 267.68$, $p < 0.01$, cheatgrass: $F = 313.11$, $p < 0.01$). In the equation for cheatgrass yield, however, the coefficient for Idaho fescue density (a measure of interspecific competition) did not differ from 0 ($t = 0.63$, $p = 0.53$). Thus cheatgrass shoot growth was not affected by neighboring Idaho fescue. With cheatgrass density as the independent variable, the model had an R^2 of 0.87; adding Idaho fescue density did not change R^2. An undisturbed-site Idaho fescue seedling grown under the conditions of this experiment and without interference

was predicted to produce 0.43 g of shoot biomass. Experimental error prevented an accurate estimate of β_0 for cheatgrass, but potential maximum shoot biomass of the alien annual was clearly much greater than that of Idaho fescue. Using the upper limit of a 95% confidence interval of β_0 (standard error = 0.15) to estimate minimum predicted dry shoot biomass of cheatgrass gave a value an order of magnitude greater (4.07 g) than Idaho fescue's predicted shoot biomass. The relative competitive ability (RC) of undisturbed-site Idaho fescue was 0.04; 25 Idaho fescue seedlings were required to provide the same intensity of interference to a target Idaho fescue as a single cheatgrass neighbor. The RC of cheatgrass was 13.10. A single cheatgrass seedling interfered with shoot growth of a neighboring cheat-

grass as much as did 13 Idaho fescue seedlings from the undisturbed site. Cheatgrass was clearly the superior competitor of the 2 species, as shown by coefficients for inter- and intraspecific competition.

Both equations were also highly significant (Table 7) for disturbed-site seedlings (Idaho fescue: $F = 927.0$, $p < 0.01$). In both models, however, regression coefficients for Idaho fescue density did not differ from 0 (Idaho fescue: $t = 0.83$, $p = 0.41$, cheatgrass: $t = 0.14$, $p = 0.89$). These results suggest that disturbed-site Idaho fescue had no competitive effect on neighboring seedlings regardless of species. Disturbed-site cheatgrass was predicted to produce as much as 94.4 g of dry shoot biomass given no interference. In comparison, predicted maximum dry weight of Idaho fescue shoot from the same sites and grown under the same conditions was 0.13 g. The RC of disturbed-site Idaho fescue was 0.008. A disturbed-site Idaho fescue seedling would have to be surrounded by 131 conspecifics to have its shoot growth inhibited to the same extent as was caused by a single cheatgrass neighbor. The RC of cheatgrass collected from the disturbed-site was 112.26. A single cheatgrass neighbor had the same influence on growth of a cheatgrass seedling as did the presence of 112 disturbed-site Idaho fescue seedlings.

Discussion

Depletion of soil moisture by a neighbor which emerged earlier usually consigns a late-emerging grass seedling to desiccation and death in sagebrush-steppe (Pyke 1990, Mack and Pyke 1984, Harris 1967). Given interference from neighboring cheatgrass, seedling establishment and recruitment into persisting Idaho fescue populations is more probable if germination is rapid (Weiner 1985, Mithen et al. 1984). However, fewer seeds from disturbed-site Idaho fescue populations germinated, they were slower to germinate, and were no less sensitive to moisture stress than were seeds from the undisturbed-site popu-

Table 4. ANOVA for Idaho fescue seed germination experiments.

	Population		Water Potential		Interaction	
	F	p	F	p	F	P
August						
Germination (%)	3.52	0.014	82.76	<0.001	NS	
Days to Germination	NS		170.14	<0.001	NS	
Median Response Time	5.65	0.001	316.83	<0.001	NS	
CRG[1]	9.12	<0.001	406.56	<0.001	3.02	0.008
September						
Germination (%)	2.56	0.051	35.31	<0.001	NS	
Days to Germination	NS		121.92	<0.001	NS	
Median Response Time	3.98	0.008	246.52	<0.001	NS	
CRG	11.86	<0.001	688.15	<0.001	NS	
October						
Germination (%)	4.03	0.007	35.68	<0.001	NS	
Days to Germination	3.49	0.015	444.65	<0.001	NS	
Median Response Time	3.15	0.023	950.08	<0.001	NS	
CRG	17.81	<0.001	745.38	<0.001	2.93	0.010

[1]CRG equals Maguire's (1962) Coefficient of the Rate of Germination.

lation. These data suggest that on alien invaded sites, seedlings from the undisturbed site have a better chance of establishing than do seedlings from disturbed sites. However, because cheatgrass seeds may begin germinating in a single day (Goodwin 1993, Thill et al. 1979), and because 5.8 to 9 days passed before Island Idaho fescue germinated, even seedlings from the undisturbed site have little chance of successfully competing with cheatgrass.

Disturbed-site Idaho fescue does not represent a more competitive ecotype. Thirteen undisturbed-site seedlings exerted the same competitive pressure on a neighboring cheatgrass as did 112 disturbed-site Idaho fescue seedlings. Resource capture, and hence competitive ability, is a function of production and positioning of resource-absorbing organs and their physiological activity (Grime 1979). Idaho fescue from the undisturbed-site had a higher growth rate and greater root length density, rooting depth, leaf area, and shoot height than conspecifics from disturbed sites. Seedlings from the undisturbed site produced 3 1/2 times the root length of disturbed-site Idaho fescue seedlings. The greatest root length achieved by any Idaho fescue seedling was 15.5 m, with a maximum rooting depth of 48 cm. Cheatgrass seedlings produced as much as 190 m of root and penetrated to a depth of 120 cm. Undisturbed-site seedlings had 2 1/2 times the root length density of disturbed-site seedlings, allowing greater

exploitation of soil resources. Root length density of cheatgrass was over 6 times that of undisturbed–site seedlings and over 16 times that of disturbed-site seedlings. Cheatgrass explored the soil intensively, producing 6.7 cm of root length for every cm^3 of soil. However, specific root length of Idaho fescue was 175% that of cheatgrass. The greater specific root length of Idaho fescue may explain why this perennial, once established, successfully competes with some alien annuals (Borman et al. 1991). If an Idaho fescue seedling survived long enough, it would accumulate suffi-

cient root length to occupy a large soil volume and successfully compete with cheatgrass for soil moisture. Our inability to detect a competitive effect of disturbed-site Idaho fescue on neighboring seedlings may reflect the large difference in sizes of cheatgrass and Idaho fescue seedlings; Idaho fescue seedlings may never have attained sufficient size to become effective competitors.

The 2 Idaho fescue groups had similar allocations to root and shoot and equivalent specific root length and specific leaf area. Körner (1991) suggested that dry matter partitioning is constant within a species, and we found no difference in root weight ratio between the 2 Idaho fescue groups. Allocation patterns differed between Idaho fescue and cheatgrass. Idaho fescue invested about 1/3 of its fixed carbon in roots, whereas roots accounted for over 1/2 of total dry biomass in cheatgrass. Despite higher specific root length of Idaho fescue, the combination of greater allocation to roots and higher growth rate gave cheatgrass a root length:leaf area ratio 1.7 times that of Idaho fescue.

The root distribution of disturbed-site Idaho fescue seedlings may reflect selection for positive geotropic root growth during nearly 100 years of competition with cheatgrass. The
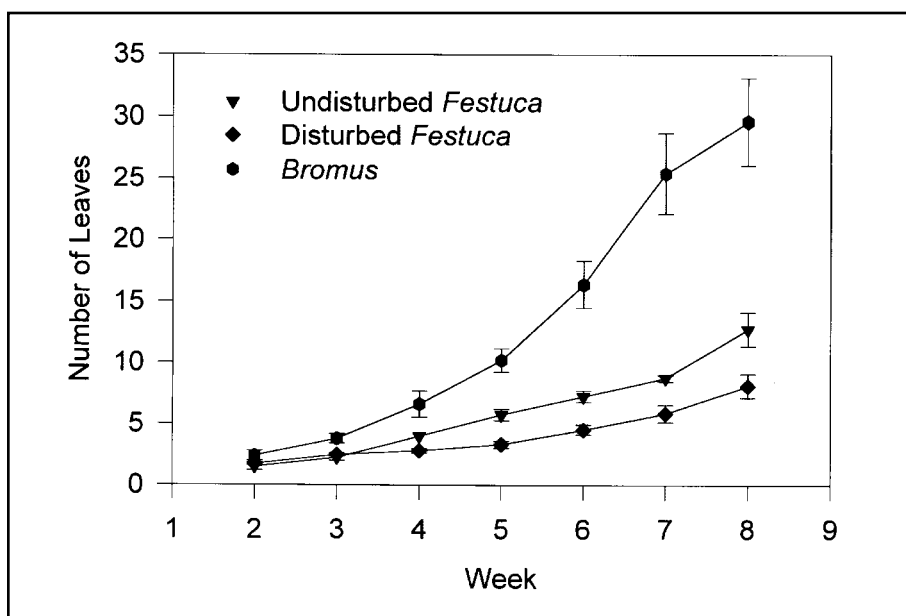

Fig. 5. Leaf production by Idaho fescue from undisturbed and disturbed sites and by cheatgrass. Plots show untransformed means and associated standard errors.

Table 5. Size and allocation patterns in Idaho fescue seedlings from disturbed and undisturbed sites and in cheatgrass seedlings.

| | Idaho fescue | | | | cheatgrass | |
| | Undisturbed[1] | | Disturbed | | | |
Variable	Mean	SE	Mean	SE	Mean	SE
Emergence (days)	7.00a	1.31	11.00b	0.66	4.80	1.31
Total Root Length (cm)	963.32a	158.10	273.09b	72.54	16,348.88	769.43
Specific Root Length (cm/g)	33,354.14a	8,061.33	31,635.85a	3,698.79	18,704.17	1,265.89
Root Length Density (cm/cm^3)	1.07a	0.19	0.40b	0.09	6.69	0.31
Total Leaf Area (cm^2)	11.66a	1.47	3.44b	0.67	125.42	6.27
Specific Leaf Area (cm^2/g)	231.86a	21.99	266.61a	10.09	226.40	9.23
Root Biomass (mg)	27.85a	3.44	8.57b	1.58	890.13	72.57
Shoot Biomass (mg)	71.15a	6.82	17.76b	3.07	707.10	43.51
Root Weight Ratio[4]	0.29a	0.05	0.33a	0.02	0.55	0.03
Root Length:Leaf Area (cm/cm^2)	78.91a	20.25	79.98a	9.29	132.52	12.30

Within a row, different letters indicate significant differences (α = 0.05)
[1]n = 4
[2]n = 19
[3]n = 5
[4]Root weight ratio = g root/g root+shoot.

availability of soil moisture in sagebrush steppe increases with depth as the growing season progresses (Link et al. 1990, Caldwell et al. 1977, Harris 1967), whereas mineral nutrients are greatest in the surface horizon (Doescher et al. 1984, Swanson et al. 1986). With less than 40% of the root length, disturbed-site seedlings extended roots to 90% of the depth attained by seedlings from the undisturbed site. Differing distributions of root biomass in the Idaho fescue groups suggest a greater emphasis on moisture uptake in disturbed-site seedlings. Another perennial grass native to sagebrush steppe, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), appears to alter root distribution in response to nutrients (Larigauderie and Richards 1994, Black et al. 1994) and neighbors (Caldwell et al. 1991). Root morphology of shrubs (*Haplopappus* spp.)

native to coastal California (USA) was altered, with fewer lateral roots at shallow depths and more at greater depths, given interference from shallowly rooted alien neighbors (D'Antonio and Mahall 1991).

Alternative Hypotheses

Given that competitive ability does not explain persistence of Idaho fescue on disturbed sites, which alternative hypothesis, reduced palatability, greater defoliation tolerance, or greater stress tolerance, appears most promising? Because livestock make heavy use (50 to 85% utilization, P. Doescher, unpublished data) of Idaho fescue on disturbed sites where grazing presently occurs, persistence is probably not due to reduced palatability. Additionally, Jaindl et al. (1994), working with a set of Idaho fescue populations that included those we

studied, found no differences in defoliation tolerance related to grazing history. Thus, hypotheses of greater competitive ability, reduced palatability, and greater defoliation tolerance have been or are likely to be rejected.

Harper (1982:15–16) noted, "No evolutionary process starts with a fresh sheet: always the process acts on ancestors that are more or less complex organized systems, and there are therefore limits on what new changes are possible....The direction of evolutinary change in a population (if any) is constrained within the limits of its genetics." Our results suggest that selective pressure due to introductions of alien plants have produced ecotypes of Idaho fescue that are more tolerant of moisture stress (sensu Grimes 1979). Invasion by cheatgrass does not result in selection for more ruderal-like genotypes of Idaho fescue, because Idaho fescue lacks the genetic potential to compete successfully with the alien (this study). Increased drought stress caused by soil moisture uptake by cheatgrass may select for genotypes more tolerant of drought stress than original Idaho fescue populations. Breeding programs designed to produce native perennial bunchgrasses for restoration of degraded western USA sagebrush-steppe should test for drought stress tolerance rather than forage production or competitive ability.

The probability of mortality is very high among perennial grass seedlings in sagebrush steppe, with up to 3 years required for establishment and a high probability of survival to the next age class (West et al. 1979). However, once established, a perennial grass may live for a long time. West et al. (1979) observed longevities of up to 43 years for individual sagebrush steppe grasses, but noted that because the period of observation was not long enough, maximum longevities could not be determined. The longevity of a sheep fescue (*Festuca ovina* L.) genotype, a species closely related to Idaho fescue, was estimated by Harberd (1962) to be as great as 1,000 years. Clonal growth (fragmentation of large individuals, see Falinska 1995, Samuel and Hart 1995) allows subsidization of new daughter tillers by

Table 6. Distribution of Idaho fescue and cheatgrass root biomass (mg) in soil columns expressed as mean root mass per stratum and as mass per cm of soil.

| | Idaho fescue | | | | cheatgrass | |
| | Undisturbed | | Disturbed | | | |
Strata (cm)	Mean[1]	per cm	Mean[2]	SE	Mean[3]	per cm
0–2	8.0a	4.0	1.8a	0.9	136.8bc	68.4
2–5	4.6b	1.5	1.6a	0.5	88.9c	29.6
5–10	6.4ab	1.3	2.2a	0.4	186.8ab	37.4
10–20	7.7a	0.8	2.2a	0.2	156.8b	15.7
20–50	3.9b	0.1	1.3a	<0.1	181.3a	6.0
50–120	0.4c	<0.1	<0.3a	<0.1	216.8a	3.1

Within a column, different letters represent significant differences (α = 0.05) determined through one-way ANOVA for each group.
[1]n = 3, SE = 0.894
[2]n = 17, SE = 0.375 except for 50–120 where n = 1 and SE = 1.547
[3]n = 5, SE = 0.0191.

Table 7. Reciprocal yield analysis of shoot production by Idaho fescue and cheatgrass seedlings from disturbed and undisturbed central Oregon sites.

Site and Species	Equation[1]	Adj. R^2
Undisturbed		
Idaho fescue	$1/W_F = 2.3268 + 0.0089N_F + 0.22N_B$	0.87
cheatgrass	$1W_C = -0.0519 + 0.007N_B + 0.0005N_F$	0.87
Disturbed		
Idaho fescue	$1/W_F = 7.638 + 0.0027N_F + 0.354N_B$	0.85
cheatgrass	$1W_C = -0.05106 + 0.0064N_B + 0.0006N_F$	0.86

[1]Subscripts identify Idaho fescue (F) and cheatgrass (B).

established tillers with well developed root systems (Marshall and Anderson-Taylor 1992, Welker et al. 1991). Such a mechanism would greatly mitigate the effects of cheatgrass on recruitment in Idaho fescue populations because ramets, in contrast to seedlings, would start their independent existence with well-developed root systems. Plasticity of established plants, including fragmentation into ramets, may have greater influence on longevity of perennial grass communities in sagebrush steppe than does seedling recruitment (West et al. 1979). The primary mechanism for adaptive change in invaded Idaho fescue populations has likely been the survival and clonal growth of individuals able to tolerate cheatgrass-intensified drought.

Additional support for our stress tolerance hypothesis was presented by Nasri and Doescher (1995). When grown in monoculture, Idaho fescue from the undisturbed-site produced 1.7 times as much shoot biomass as disturbed-site populations. Addition of 5 cheatgrass seedlings reduced shoot biomass in the undisturbed population by 35%, but did not reduce shoot biomass in disturbed-site populations. Shoot biomass was reduced in all Idaho fescue when grown with 10 cheatgrass neighbors: by an additional 30% in the undisturbed population and 32% in disturbed-site populations. It is incorrect to interpret the constant shoot biomass of disturbed-site Idaho fescue when grown in monoculture and at the lower cheatgrass density as evidence of greater competitive ability. A slow, largely invariable rate of growth accompanies stress-tolerance (Grime 1979). The capacity for rapid production of roots and leaves, and quick morphological adjustment in response to transient resource enrichment, confers competitive ability (Grime 1979), and resource capture and competitive success increase with leaf and root surface area (e.g. Weiner 1985, Gross 1981). A competitive plant would be expected to produce biomass quickly when grown without interference, as did Idaho fescue from the undisturbed-site and as disturbed-site Idaho fescue did not.

We believe Idaho fescue has persisted on grazed and invaded sagebrush-steppe because of greater drought stress tolerance, not greater competitive ability. Disturbed-site Idaho fescue populations likely represent stress tolerant ecotypes resulting from intensified selection pressures, due to introductions of alien species, operating within genetic constraints imposed by ancestors. Our results suggest that frequent recruitment of Idaho fescue seedlings is improbable on invaded sites, and persistence of these populations requires longevity of established genotypes or recruitment of new individuals or both. Seeds remain important to long-term survival and evolution of the populations because of new genotypes generated through sexual reproduction. However, between episodes of seedling recruitment, clone formation by adapted genotypes is, we believe, key to the persistence of Idaho fescue on invaded sagebrush-steppe. Understanding the population biology of Idaho fescue and other native perennial grasses provides a foundation for proper rangeland management, having implications that extend from sustainable grazing management to conservation and restoration.

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