Idaho fescue (*Festuca idahoensis* Elmer) is a native, perennial, cool-season bunchgrass and is an excellent forage for both wild and domesticated ungulates. Heavy and continuous grazing following settlement has reduced densities of Idaho fescue on central Oregon rangelands. Additionally, invasion of these rangelands by competitive alien annuals, such as cheatgrass (*Bromus tectorum* L.), has caused Idaho fescue populations to decline because recruitment of seedlings is largely prevented.

Despite the presence of alien annuals and over a century of abusive grazing, populations of Idaho fescue still grow on central Oregon rangelands, and these populations are not limited to refugia inaccessible to livestock or areas not invaded by cheatgrass. A series of experiments was completed to answer the question of why these populations still persist in central Oregon. The basic hypothesis was: remnant populations of Idaho fescue persisting on grazed and invaded central Oregon rangelands represent a competitive ecotype. Experiments compared germination requirements, root and shoot growth, and competitive abilities of Idaho fescue collected from an ungrazed relict area, four populations found on degraded sites, and
cheatgrass (also from the same four degraded sites). After-ripening requirements of Idaho fescue seed were also investigated.

In the germination experiments, Idaho fescue and cheatgrass germinated well under conditions simulating August, September, and October in central Oregon. Seed from the relict population of Idaho fescue germinated faster and more completely than did the disturbed-site seed in all three experiments. Cheatgrass germinated faster than did any of the five Idaho fescue populations. The temperature regime used in the September experiment (4/23 °C) was the most favorable. Warmer (August) and cooler (October) temperatures inhibited germination compared to September temperatures, though responses differed between the two species. Increasing water stress (adjusted osmotically) inhibited Idaho fescue seed germination and slowed cheatgrass seed germination. Persistence of Idaho fescue on grazed, cheatgrass-invaded sites is not due to germination in the disturbed populations that mimics cheatgrass.

After-ripening requirements of Idaho fescue were investigated in a second experiment. Idaho fescue seed required six months of after-ripening before the maximum potential for germination was realized. Storage of dry seed at either room temperature (20 °C) or cooler, alternating temperatures (5/15 °C) did not alter the rate at which dormancy was lost. Because seed shatter occurs in late July and early August for Idaho fescue, a six month after-ripening requirement insures the greatest potential germination coincides with the spring period most likely to provide sufficient soil moisture for seedling establishment. Additionally, seed longevity varied greatly from year to year; Idaho fescue seed produced in a very dry year had poorer
germination and shorter longevity than seed produced during a year with near normal precipitation.

Hypotheses of greater rates of root and shoot growth, greater allocation to roots, and more efficient production of biomass in Idaho fescue seedlings from disturbed sites compared to relict-site seedlings were tested in a third experiment. Relict-site seedlings emerged earlier, grew faster, and produced more resource-absorbing root length and leaf surface than disturbed-site seedlings. Root biomass distributions were different as well. Relict-site seedlings had 52% of their root biomass in the upper 0-2 cm of the soil column. Seedlings from disturbed sites had 42% of their root biomass in the surface horizon. Both groups, however, had 60% of their root biomass in the upper 10 cm of the soil column. Disturbed-site seedlings produced only 40% as much root length as seedlings from the relict-site, but extended roots to 90% of the depth attained by the faster growing relict-site seedlings. However, the two Idaho fescue groups had equivalent specific leaf areas, specific root lengths, and root weight and root length:leaf area ratios. Cheatgrass emerged earlier, grew faster, and had greater root length and leaf area than did Idaho fescue. Allocation to roots was greater in cheatgrass than in Idaho fescue, and the alien produced roots which penetrated deeply into the soil column. The surface horizon held 42% of cheatgrass root biomass, and over 60% was at depths greater than 10 cm. Specific leaf areas of Idaho fescue and cheatgrass were similar. However, specific root length of cheatgrass was ¼ less than that of Idaho fescue. On a per unit biomass basis, Idaho fescue was more efficient in root production. Greater allocation to roots and faster growth in cheatgrass resulted in a root length:leaf area
ratio that was almost double that of Idaho fescue. Persistence of Idaho fescue on cheatgrass-invaded rangelands is not due to greater ability to compete for soil moisture.

Competitive abilities of Idaho fescue seedlings from the disturbed-site and relict populations were investigated by growing the seedlings in replacement series with cheatgrass (plus additional monocultures over a range of densities). Reciprocal yield analysis gave results that supported earlier findings: the Idaho fescue population from the relict-site competed with cheatgrass for resources more successfully than the disturbed-site populations. Though cheatgrass was largely unaffected by interference from Idaho fescue, the regression coefficient quantifying interspecific competition was greater for cheatgrass grown with relict-site Idaho fescue than for any other Idaho fescue population. Cheatgrass growth was most affected by neighboring conspecifics. Idaho fescue growth was more strongly influenced by interspecific competition than by competition from conspecifics. For cheatgrass and Idaho fescue, regression coefficients for Idaho fescue density were often not significantly different from zero. Only in the equation describing the response of Idaho fescue from the relict site was the density of Idaho fescue significant. The relative competitive ability (RC) of Island Idaho fescue was 0.041, whereas that of the disturbed-site populations taken together was 0.008. Cheatgrass had an RC many times greater than that of any Idaho fescue population. Cheatgrass seedlings were also theoretically capable of producing far more shoot biomass than Idaho fescue if grown without interference.

The persistence of Idaho fescue on degraded central Oregon rangelands is not due to greater competitive ability in these populations relative to a relict population.
It may be that greater stress tolerance in the disturbed-site populations is the reason for their continued existence, and the results of these investigation may be interpreted to support this idea. A species which evolved in a relatively depauperate, drought-prone environment will likely have adaptations that improve stress tolerance over competitive ability.
Ecotypic Variation, Adaptation, and Persistence of Idaho Fescue on Degraded Central Oregon Rangelands

by

Jay Rodney Goodwin

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Completed 24 August 1993
Commencement June 1994
Acknowledgements

I'd like to thank James Michener and Herman Wouk for ghost-writing this thesis. Without their assistance, it would have been much shorter.

Thanks to Paul Doescher for his unflagging support and encouragement. Paul's door was always open, and he was always willing to listen to questions and offer ideas. I can recommend Paul as a major professor for any prospective graduate student without the slightest reservation, even if he is a slasher. I have really enjoyed working with you Dr. Paul.

Thanks to the one and only Dodi Reesman, department secretary extraordinaire. You made the difficult task of writing a thesis much more tolerable. Thanks for all your help, for checking my e-mail, relaying messages, and getting me that coupon for the electronic dictionary. I'll remember you in my will.

A big thanks to Dr. Kim Hummer, my boss at the USDA ARS National Clonal Germplasm Repository, who gave me the freedom that enabled the completion of this thesis. Kim allowed me to take an extraordinary amount of leave without pay, without losing my job, so that I could write this tome. Kim supported and encouraged me though it meant I devoted less time to the job she hired me to do. I truly appreciate all you did for me, Kim. Thanks also to the rest of the repository folks who were undoubtedly inconvenienced by my absences yet put up with me.

Thanks to Dr. Donald Zobel for serving on my committee, writing letters of recommendation, and encouraging me in my pursuit of first a B.S., then a M.S. Your compliments for good work and critiques of a shoddy performance have meant a lot to me. I am a better researcher and writer because of you.

A similar thanks to Dr's Lee Eddleman and Ed Starkey for encouragement, letters of reference, and performing the onerous task of serving on my committee and reading every word of this thesis. I wish I could have osmotically absorbed all the knowledge of these two exceptional 'big picture' ecologists.

Thanks to Dr. Dave Thomas of the Department of Statistics, who (on short notice) took the time to write a SAS program for a repeated measures ANOVA. I had purposefully avoided SAS because of the steep learning curve, and Dr. Thomas got me over a bump that could have been very unpleasant otherwise.

A truckload of gratitude for my father, Dr. D.L. Goodwin. Without your support ($$$) and encouragement I'd still be working a minimum wage job somewhere. Who would have thought that the kid who kept complaining every time you dragged us out into yet another sagebrush flat would follow in your footsteps. I never did, that's for sure.

An equally large thanks to my mother, Naida L. Goodwin, for encouragement, hard-to-come-by dollars, and chocolate chip cookies. You're the best, mom.

Thanks also to Ardle and Colleen McConnell, my wife's parents. For economic reasons (the Great Depression followed by World War II), neither Mac nor Colleen finished high school, and their pride in their daughter's, and her husband's, scholastic accomplishments has been literally tangible. Thanks to you both for the financial support you've given us, particularly during the last six months when I was barely working. I'm starting a Ph.D. in September Mac; there may be a doctor in family after all.
Thanks to Mohammed Nasri, Rodger Sheley, Mack Barrington, Judy Vergun and the other graduate students who have offered their friendship and assistance. Rodger in particular showed what it means to use a sharp mind creatively. Thanks for the examples, Rodger.

Thanks to a dear friend, Karen Tressler, who promised to annoy me to death if I didn't acknowledge her support and encouragement through this whole thing. I really appreciated the thoughtful gifts (Open on the morning of your defense, Open after your defense as your committee deliberates, Open after the committee's decision). You beat me to a Master's Karen, but mine's still better. It's your turn, Tim.

Lastly, I'd like to thank my smart, charming and beautiful wife, Erin McConnell. When things got tough and I got tense and curt and distant, she put up with me, helped me through it, and got my feet back on the ground where they belong. I can really be unpleasant sometimes, especially when trying to figure out some new statistical procedure that I have to use because my data wouldn't satisfy the assumptions behind other procedures (aarrrgghhh!), but Erin tolerated me no matter how bad I got. Truly, she's been a saint. I owe you big-time, Erin. Thanks a galaxy. I hope to do the same for you when you do your M.S.
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Ecotypic Variation, Adaptation, and Persistence of Idaho fescue on Degraded Central Oregon Rangelands.

CHAPTER I. INTRODUCTION
Ecotypic Variation, Adaptation, and Persistence of Idaho fescue on Degraded Central Oregon Rangelands.

Introduction

As a result of abusive grazing, inappropriate agricultural practices, the introduction of alien plants, and fire suppression, the abundance and diversity of native bunchgrass species on rangelands of the Intermountain West have been reduced (Anon. 1972; Young et al. 1987). Soil erosion has been greatly accelerated, and in cases the A horizon has been removed (West 1988). Reseeding remains one of the primary strategies for improving degraded rangelands. Unfortunately, the supply of native seed is very limited and rangeland reseeding programs often achieve little success (defined here as the establishment and persistence of populations of the seeded species) (Klomp and Hull 1972; Harris and Goebel 1986; Vallentine 1989). A major factor in the failure of reseeding efforts is the extremely variable and unpredictable climate of Intermountain rangelands. Drought is common. Annual precipitation averages about 25 cm (Hidy and Klieforth 1990). Summers are warm and winters cold. For example, extreme temperatures of 41 and -37 °C have been recorded in central Oregon (Anon. 1981-1989). Diurnal temperature fluctuations are great, even in winter, and freezing temperatures are possible in any month of the year. Plant growth is largely dependent upon soil moisture accumulated during late fall to early spring. Brief, intense thunderstorms during the growing season usually do not benefit plants because little rain infiltrates the soil (West 1988). Another factor contributing
to the failure of seedings is interference from introduced annuals, such as cheatgrass (*Bromus tectorum* L.). The control of alien invaders and maintenance of ecological integrity and biodiversity will remain one of the most pressing challenges facing managers of natural resources in the future (Soule 1990; Noss 1990; Westman 1990; Brussard 1991).

Idaho fescue (*Festuca idahoensis* Elmer) populations persist on degraded central Oregon rangelands colonized by cheatgrass, and may represent an ecotype capable of successfully competing with alien species. Past research has demonstrated the ability of this species to develop ecotypes. In common garden experiments, Tisdale (1959, 1961) found Idaho fescue to have great genetic variability, with collections from different geographic areas and habitat types showing differences in phenology and morphology. Doescher (1983) concluded that Idaho fescue in communities dominated by ponderosa pine represented a different ecotype than that found in sagebrush-dominated communities. Ecotypes capable of rapid root growth at low soil temperatures offer the greatest potential for re-establishing native perennial grasses on cheatgrass dominated sites (Harris 1967).

I tested the hypothesis that remnant populations of Idaho fescue persisting on degraded central Oregon rangelands are genetically adapted to compete successfully with cheatgrass. If my principal hypothesis were true, this research would provide a basis for the breeding and subsequent re-establishment of this and possibly other native perennial grass species on semi-arid rangelands. Westman (1990) noted the need for basic research into the functioning of "mixed exotic-native ecosystems" to
better understand competition and the evolution of plant assemblages. Predicting the impact of invaders on ecosystem structure and function rests upon such research, as does the maintenance of biodiversity (Westman 1990; Brussard 1991). Soule (1990:235) argued, "The control and extirpation of damaging aliens, especially species like fire-conducting grasses, will remain among the most urgent of all management activities."

Re-establishment of perennial grass species on degraded rangelands, coupled with proper livestock management, would aid in reversing the existing trend of declining range condition and desertification, improve site water relations, increase wildlife and livestock carrying capacities, and enhance the aesthetic qualities and recreational value of the range landscape. Additionally, a basis for the conservation of biological diversity given global warming, and the resultant climate shifts and perturbation of biotic communities, may be provided (Westman 1990; Harrington 1987; Peters and Darling 1985).

Experimentation focused on germination and growth responses under environmental conditions representative of late summer and fall in central Oregon. Comparisons were made of germination, seedling growth, and competitive ability of Idaho fescue collected as seed from a relatively undisturbed relict area, the Island (Driscoll 1964), and degraded sites in central Oregon, both independently and with interference (Harper 1977) from cheatgrass. I sought the greatest degree of realism possible in my experiments, in order to obtain results that would apply in a field situation. Bainbridge and Virginia (1990) noted that ecological restoration is often
hastened when treatments simulate natural environmental conditions (soil properties, temperature and moisture regimes) that would be found if the restoration site supported a healthy system.

Literature Cited


CHAPTER II. DESCRIPTIONS OF CLIMATE, COLLECTION SITES, AND STUDY SPECIES.
The Climate of Central Oregon

The climate of a region greatly influences its vegetation; climate defines the macro-scale boundaries within which vegetation occurs (Walter 1985; Woodward 1987). Plants are directly affected by microclimate, and micro-scale environmental data are preferred when studying a species' autecology. However, when microclimate data are not available, macro-scale climate data should be considered. Macro-scale extremes are likely much more moderate than are extremes on the micro-scale. For example, macroclimate temperature data are collected 1 m above the soil surface, yet diurnal temperature fluctuations are greatest at the soil surface. Reflecting the significant role of climate in the ecology of plants, I will discuss the macroclimate of the central Oregon area. Because this study focused on the germination and seedling ecology of Idaho fescue and cheatgrass during autumn, the discussion of climate primarily concerns the fall period.

This discussion focuses on the roughly triangular area bound on the southwest by Redmond, by Madras to the northwest, and by Prineville to the east in central Oregon (figure 2.1). Central Oregon has a semiarid continental climate featuring cold, moist winters and hot, dry summers. Based on 38 year climate records from the stations of Redmond, Prineville, and Madras (Anon. 1983, 1981-89), mean annual temperature is 8.8 °C and mean annual precipitation is 270 mm. Over half (55.4%) of this precipitation falls during November to March when air temperatures are generally 5 °C or less, and a measurable snowpack is typical for this period.
Figure 2.1 Map of Oregon and locations of the Redmond, Prineville, and Madras climate stations and the Idaho fescue seed collections sites: 1 The Island, 2 Blanchard, 3 Lone Pine, 4 McCoin, and 5 Combs Flat.
Snowfall is common in October, and an average of 5.3 cm of snow is on the ground by November. Snowpack is greatest in January, averaging about 14 cm. By April,
most of this snow has melted and infiltrated the soil. Summers are typically droughty (figures 2.2 - 2.4). Summer precipitation is generally delivered during brief, intense thunderstorms which produce overland flow instead of infiltration (West 1988). The average growing season lasts about 100 days. The region has great diurnal
temperature fluctuations and highly variable precipitation during late summer and fall.

Day length is appreciably shorter in November than in August, and mean monthly

temperatures reflect the reduced radiant energy input.
The effective environment of plants in the study area changes appreciably between August and November. In general, August temperature and light regimes favor growth, but available moisture is limiting. September and October are likely to be more moist than August, but available moisture is still limited, day length shorter, and temperatures may be cool. Growth is probably inhibited during November by low temperatures.

Relatively infrequent anomalous events, such as a wet August, are probably required for establishment of Idaho fescue in central Oregon during the late summer and fall. In perennial rangeland grasses, seedling establishment and survival to reproductive maturity appears to be limited to infrequent years of exceptionally favorable environmental conditions, despite an annual input of seeds (Weaver and Mueller 1942; Doerr et al. 1984). Such "pulse" recruitment has been suggested for plant populations in arid and semiarid regions (e.g. Young et al. 1990; Bainbridge and Virginia 1990; West et al. 1979).

Temperature and Precipitation Tables 2.1–2.3 present climatological data for the months of August, September, and October for Redmond, Prineville, and Madras, Oregon based on a 38 year record (Anon. 1983, 1981-1989). Dr. Lee Eddleman (pers. comm.) has suggested that, of the three recording stations, Redmond best represents the temperature regimes of high plateaus in the study area where Idaho fescue is found. The Madras and Prineville stations are at lower elevations.
August is generally the warmest and driest month, averaging 18.7 °C and 9 mm precipitation. Both September and October are cooler and wetter, averaging 13.0
Table 2.3 Temperature and precipitation data for Madras, Oregon¹.

<table>
<thead>
<tr>
<th>Month</th>
<th>August</th>
<th>September</th>
<th>October</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>19.30 (±1.07)</td>
<td>14.18 (±1.45)</td>
<td>9.32 (±0.80)</td>
</tr>
<tr>
<td>Mean Maximum</td>
<td>31.07 (±1.45)</td>
<td>24.54 (±2.57)</td>
<td>19.24 (±2.73)</td>
</tr>
<tr>
<td>Mean Minimum</td>
<td>x.50 (±1.03)</td>
<td>3.80 (±0.98)</td>
<td>0.03 (±0.71)</td>
</tr>
<tr>
<td>Precipitation (mm)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>10.33 (±15.84)</td>
<td>17.72 (±15.46)</td>
<td>18.65 (±16.57)</td>
</tr>
<tr>
<td>Wet Month</td>
<td>14.46</td>
<td>24.81</td>
<td>26.11</td>
</tr>
<tr>
<td>Dry Month</td>
<td>6.20</td>
<td>10.63</td>
<td>11.19</td>
</tr>
</tbody>
</table>

¹ Values in parentheses are standard deviations.

and 9.2 °C and 16.5 and 17.8 mm precipitation, respectively. Precipitation is more
reliable in the latter months than in August. In both September and October,
precipitation means are larger than their associated standard deviations; in August, the
mean is smaller than its standard deviation. November is wetter still than the
preceding months but is also considerably cooler, averaging 38.3 mm precipitation
and a temperature of 3.4 °C. Though November moisture would favor plant growth,
low temperatures would greatly inhibit production.

The average difference between monthly mean maximum and minimum
temperatures is 17 °C, and fluctuations are greatest during the late summer and least
in winter. Diurnal fluctuations average 23, 21, and 19 °C during August, September,
and October, respectively (figure 2.5). Temperature fluxes remain relatively large in
winter, averaging 12 °C in November and 10 °C in December.
Precipitation in central Oregon is highly variable on both spatial and temporal scales (figure 2.6). The data pictured span a ten year period for Redmond, and is representative of this region. During this decade, Redmond averaged more fall precipitation than during the 38 year period of 1951 to 1989. Prineville received less precipitation during the fall than the long term average, while Madras was near normal.

**Insolation** Insolation data are not available for Redmond, Prineville, or Madras. However, solar radiation data have been collected at Burns since 1979 (Anon. 1989). These data should be indicative of the study area as all four locations are at roughly equivalent latitudes and have similar climates. Data for total solar (global) radiation received at the ground surface in Burns (Anon. 1989) were used to estimate photosynthetically active radiation (PAR) levels during the late summer and fall. The proportion of global radiation that is photosynthetically active is nearly constant at 0.5 (±0.02) (Szeicz 1974 cited in Fitter and Hay 1987). To convert from photosynthetic irradiance (watts/meter²) to the corresponding photosynthetic photon flux density (PPFD, units are Einsteins), a factor of 1 W/m² = 4.6 µE/m²s was used (McCree 1972). Daily light integrals were calculated from midday instantaneous PPFD values using a conversion factor of 1 µE/m²s = 0.02 E/m²d (Foggo 1986).

Of the months of interest, day length and solar elevation are greatest in August and least in November; correspondingly, irradiance is greatest in August and
Figure 2.5 Hourly mean temperature during late summer and fall at Redmond, Oregon based on three years’ data (1986-1988).

Figure 2.6 Variation in monthly precipitation during late summer and fall at Redmond, Oregon.
decreases as the season advances (table 2.4). Figure 2.7 illustrates hourly PAR levels over a twenty-four hour period for each of the months of interest.

Table 2.4 Daily mean irradiance at Burns, Oregon, 1979-1988.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean Total Solar Radiation</th>
<th>Photosynthetic Irradiance</th>
<th>Daily Light Integral</th>
</tr>
</thead>
<tbody>
<tr>
<td>August</td>
<td>6370</td>
<td>3185</td>
<td>36.94</td>
</tr>
<tr>
<td>September</td>
<td>4870</td>
<td>2435</td>
<td>30.13</td>
</tr>
<tr>
<td>October</td>
<td>3220</td>
<td>1610</td>
<td>21.71</td>
</tr>
<tr>
<td>November</td>
<td>1720</td>
<td>860</td>
<td>13.29</td>
</tr>
</tbody>
</table>

1. Units are watts/meter²  2. Units are Einsteins/meter² day

Figure 2.7 Hourly mean quantum flux at Burns, Oregon, during late summer and fall based on 10 years’ data (1979-1988).
The Collection Sites

Soil surveys prepared by the USDA Soil Conservation Service (SCS) (Mayko and Smith 1966; Green 1975), where available, were used to describe the edaphic properties of the collection sites. Soil properties of the Combs Flat study site did not match those of the mapping unit for the area, so I used the soil series that most closely conformed to my observations. The only published soil survey of the Island appears in Driscoll (1964). Additionally, soil samples were collected from the surface horizon (0-5 cm) at each collection site, once in spring (June) and once in autumn (August and September), and analyzed by the Soil Testing Laboratory of Oregon State University (table 2.5).

The vegetation of each site was sampled in summer (25 and 26 July, 1993), using ten 50 x 50 cm plots placed every 1.5 m along a 15 m transect. Cover by species, plant litter, woody debris, cryptogamic crust, bare ground, and rocks, was visually estimated (Daubenmire 1959 cited in Barbour et al. 1987). The number of rooted plants of a given species was tallied in each quadrat to measure density. The desire to sample all five sites in the same period, so as to avoid differences in plant phenologies, coupled with the demands of a regular Monday-Friday job, necessitated completion of the surveys in a single weekend. This constraint limited the number of transects to one per site rather than a preferred four per site.

I attempted to include as great a degree of randomness in locating the transects as possible. To layout a transect, I first positioned myself in the subjective “middle”
Table 2.5 Soil chemical properties\(^1\) of the surface horizon (0-5 cm) for the five Idaho fescue collection sites and the study plot\(^2\).

<table>
<thead>
<tr>
<th>Site</th>
<th>pH</th>
<th>P</th>
<th>K</th>
<th>NO(_3)-N</th>
<th>NH(_4)-N</th>
<th>OM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>6.60</td>
<td>22.5</td>
<td>441.0</td>
<td>1.735</td>
<td>4.025</td>
<td>3.17</td>
</tr>
<tr>
<td>Combs Flat</td>
<td>6.75</td>
<td>22.5</td>
<td>380.5</td>
<td>0.525</td>
<td>3.760</td>
<td>4.32</td>
</tr>
<tr>
<td>McCoin Orchard</td>
<td>6.60</td>
<td>17.5</td>
<td>353.0</td>
<td>1.710</td>
<td>4.560</td>
<td>8.26</td>
</tr>
<tr>
<td>Blanchard</td>
<td>6.75</td>
<td>19.5</td>
<td>345</td>
<td>0.545</td>
<td>3.780</td>
<td>3.98</td>
</tr>
<tr>
<td>Lone Pine</td>
<td>6.90</td>
<td>20.0</td>
<td>637.5</td>
<td>0.635</td>
<td>3.565</td>
<td>7.25</td>
</tr>
<tr>
<td>Study Plot</td>
<td>6.95</td>
<td>22.0</td>
<td>495.5</td>
<td>1.620</td>
<td>3.510</td>
<td>2.74</td>
</tr>
</tbody>
</table>

1. Nutrient concentrations are mg/Kg; organic matter is expressed as a percentage. 2. n=2

of the sites where Idaho fescue seed had been collected. I then randomly determined the starting point and direction of the transect. The procedure was modified for the Blanchard site, where Idaho fescue is limited to a linear strip adjacent to a fence. At Blanchard, the point at which the transect started was chosen randomly, but the direction of the transect was prescribed by the fence row. In the discussion of the plant community found at each collection site, I have emphasized cover. Cover gives an indication of the degree of influence on site microenvironment and resource capture exercised by a species.

**McCoin Orchard** The McCoin Orchard Idaho fescue population occurs on a north exposure of moderate slope. The soil is a Prag cobbly loam (PrE), a well-drained upland soil derived from rhyolitic parent material. Prag soils are found between the elevations of 1067-1372 m on slopes ranging between 5-50 %. A Prag cobbly loam profile has a dark-gray cobbly loam surface horizon of neutral pH that
extend to a depth of about 23 cm. The underlying subsoil is a brown cobbly loam about 66 cm thick and mildly alkaline. Between the depths of roughly 89 and 100 cm is a moderately alkaline, brown, very cobbly clay. Partially consolidated tuff sediment occurs at depths greater than 100 cm. Permeability of Prag soils is slow, giving a moderate potential for surface runoff and erosion. This soil is capable of supplying 15-23 cm of moisture over the growing season. Available water holding capacity is only 7.5-15 cm of moisture, however, meaning plant growth would be significantly reduced by a lack of moisture during a dry spring. The average rooting depth in Prag soils is 50-100 cm. Spring growth on sites having Prag soils generally starts in mid- to late-March.

The historic climax community of North Exposure range sites, of which the McCoin Orchard site is an example, was almost entirely herbaceous, with Idaho fescue usually the dominant species. Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith) and Sandberg’s bluegrass (*Poa secunda* Presl) were also very common, and perennial forbs, including yarrow (*Achillea millefolium* L.), milkvetch (*Astragalus* spp.), and lupine (*Lupinus* spp.), were well represented. Perennial shrubs, such as green rabbitbrush (*Chrysothamnus vicidiflorus* (Hook.) Nutt.), wax currant (*Ribes cereum* Dougl.), bitterbrush (*Purshia tridentata* (Pursh) DC.), serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt.), and buckwheat (*Eriogonum* spp.), were present at low densities.

The McCoin site has been invaded by western juniper (*Juniperus occidentalis* Hook.) (table 2.6, table 2.7). Idaho fescue remains the dominant bunchgrass, though
cover by Sandberg’s bluegrass is comparable. Bluebunch wheatgrass is well represented also, but has the lowest cover of the three bunchgrasses. Cheatgrass cover is less than 1%.

**Lone Pine** The Idaho fescue population at Lone Pine is found on a northwestern exposure of moderately steep slope. The soil of the Lone Pine site is mapped as an undifferentiated mix of Curant and Tub silt loams. This mapping unit consists of 55-75% Curant soils and 15-30% Tub soils. Curant soils developed from loess, whereas Tub soils have calcareous colluvium for a parent material. Both are well-drained, upland soils and are common on northwest exposures. These soils are found between the elevations of 670 and 1200 m on 40-70% slopes. Because of deep, well-developed soils, this site likely supports greater plant growth during a spring drought than either the McCoin or Blanchard sites. Steep slopes and moderate to slow infiltration give a high potential for surface runoff and erosion.

A representative Curant profile has a dark-gray silt loam surface horizon of neutral pH that extends to 40 cm. This is underlain by a mix of brown silt loam and heavy silt loam that is mildly alkaline and averages 45 cm in thickness. The final horizon is a moderately alkaline, pale-brown silt loam that extends down another 70 cm. Permeability is moderate, and Curant soils can supply 23-30 cm of moisture over the growing season. Between 20 and 25 cm of available moisture can be held by this soil. This is a deep soil and plants root to depths of 60 cm and more.
Table 2.6 Cover (%) by plant species, bare ground, litter, and rocks at the five collection sites.

<table>
<thead>
<tr>
<th>Species</th>
<th>Island</th>
<th>McCain</th>
<th>Blanchard</th>
<th>Lone Pine</th>
<th>Combs Flat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juniperus occidentalis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>2</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agropyron spicatum</td>
<td>6</td>
<td>2</td>
<td>3</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Festuca idahoensis</td>
<td>6</td>
<td>8</td>
<td>7</td>
<td>2</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Poa secunda</td>
<td>6</td>
<td>&lt;1</td>
<td>3</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Poa cusickii</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poa sp.</td>
<td></td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>1</td>
<td>&lt;1</td>
<td></td>
<td>&lt;1</td>
<td></td>
</tr>
<tr>
<td>Koeleria cristata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&lt;1</td>
</tr>
<tr>
<td>Stipa columbiana</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stipa sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vulpia octoflora</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vulpia bromoides</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td></td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>&lt;1</td>
<td>11</td>
<td>&lt;1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Bromus mollis</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bromus comutatus</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Achillea millefolium</td>
<td>&lt;1</td>
<td>1</td>
<td></td>
<td>&lt;1</td>
<td></td>
</tr>
<tr>
<td>Holostewn umbellatum</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td></td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Polygonum heterosepalum</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arabis sp.</td>
<td>&lt;1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepidium sp.</td>
<td>&lt;1</td>
<td>1</td>
<td></td>
<td>&lt;1</td>
<td></td>
</tr>
<tr>
<td>bare ground</td>
<td>59</td>
<td>23</td>
<td>3</td>
<td>71</td>
<td>17</td>
</tr>
<tr>
<td>rock</td>
<td>1</td>
<td>2</td>
<td>32</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>litter</td>
<td>12</td>
<td>57</td>
<td>6</td>
<td>17</td>
<td>63</td>
</tr>
<tr>
<td>woody debris</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>&lt;1</td>
</tr>
<tr>
<td>cryptogamic crust</td>
<td></td>
<td>9</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. n=10 for all mean cover values.
Table 2.7 Density of plant species at the five collection sites\textsuperscript{1}.

<table>
<thead>
<tr>
<th>Species</th>
<th>Island</th>
<th>McCoin</th>
<th>Blanchard</th>
<th>Lone Pine</th>
<th>Combs Flat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juniperus occidentalis</td>
<td>---</td>
<td>0.4</td>
<td>0.8</td>
<td>0.8</td>
<td>0.8</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>0.4</td>
<td>---</td>
<td>0.8</td>
<td>---</td>
<td>0.4</td>
</tr>
<tr>
<td>Agropyron spicatum</td>
<td>4.0</td>
<td>3.2</td>
<td>11.6</td>
<td>1.2</td>
<td>1.2</td>
</tr>
<tr>
<td>Festuca idahoensis</td>
<td>3.6</td>
<td>6.4</td>
<td>6.4</td>
<td>3.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Poa secunda</td>
<td>---</td>
<td>40.8</td>
<td>3.6</td>
<td>24.4</td>
<td>45.6</td>
</tr>
<tr>
<td>Poa cusickii</td>
<td>18.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Poa sp.</td>
<td>---</td>
<td>0.8</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>---</td>
<td>5.6</td>
<td>0.8</td>
<td>---</td>
<td>0.8</td>
</tr>
<tr>
<td>Koeleria cristata</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0.4</td>
<td>---</td>
</tr>
<tr>
<td>Stipa columbiana</td>
<td>4.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Stipa sp.</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>0.8</td>
<td>---</td>
</tr>
<tr>
<td>Vulpia octoflora</td>
<td>9.6</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Vulpia bromoides</td>
<td>---</td>
<td>4.8</td>
<td>---</td>
<td>45.6</td>
<td>24.0</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>---</td>
<td>6.0</td>
<td>254.0</td>
<td>11.2</td>
<td>254.4</td>
</tr>
<tr>
<td>Bromus mollis</td>
<td>---</td>
<td>2.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Bromus comutatus</td>
<td>---</td>
<td>---</td>
<td>1.2</td>
<td>---</td>
<td>0.4</td>
</tr>
<tr>
<td>Achillea millefolium</td>
<td>---</td>
<td>0.4</td>
<td>3.2</td>
<td>---</td>
<td>4.4</td>
</tr>
<tr>
<td>Holosteum umbellatum</td>
<td>---</td>
<td>12.0</td>
<td>---</td>
<td>6.0</td>
<td>30.4</td>
</tr>
<tr>
<td>Polygonum heterosepalum</td>
<td>---</td>
<td>2.0</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Arabis sp.</td>
<td>---</td>
<td>1.6</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Lepidium sp.</td>
<td>---</td>
<td>---</td>
<td>8.4</td>
<td>186.8</td>
<td>13.6</td>
</tr>
</tbody>
</table>

\textsuperscript{1} n=10 for all mean density values; density expressed as plants/m\textsuperscript{2}.

The Tub profile has a neutral surface horizon that is a gray, silt loam 5-30 cm thick. Below the surface horizon is a horizon of mixed clay loam and clay that
extends to a depth of about 50 cm and is mildly alkaline. The next horizon is a moderately alkaline, pale-brown, gravelly silty clay and gravelly clay loam and is roughly 40 cm thick. A white, cobbly loam is encountered at depths greater than 95 cm. Permeability is slow. Tub soils can provide 15-23 cm of moisture over the growing season, and can hold 8-18 cm of water. Spring growth starts in late March.

The Lone Pine site is classified as a Steep North range site. The historic climax community of this range site was strongly dominated by herbaceous species with Idaho fescue being the most common. Bluebunch wheatgrass and Sandberg’s bluegrass were also well represented in the community. Yarrow, milkvetch, lupine, and other perennial forbs were common. The shrub component, consisting of green rabbitbrush, rose (Rosa spp.), bitterbrush, wax currant, snowberry (Symphoricarpos albus (L.) Blake), and others, was represented by individuals at low densities.

Western juniper has invaded the Lone Pine site, and Sandberg’s bluegrass has become the dominant bunchgrass (table 2.6, table 2.7). Cover by Idaho fescue is slightly lower than that of the dominant bluegrass, and bluebunch wheatgrass cover is less than half that of Idaho fescue. Cheatgrass cover is less than 1 %.

**Blanchard** The Blanchard Idaho fescue population is largely restricted to a fence line that parallels a gravel road. Idaho fescue occurs in the strip between road and fence, and on the pasture side of the fence where a row of piled rocks make the plants inaccessible to cattle. The site has a very gentle slope. The soil of the site is a Gribble cobbly loam (GrD), which is a well-drained upland soil formed from rhyolitic
colluvium. The Gribble series is found between the elevations of 1000 and 1050 m on slopes of 5-20%. A representative profile has a dark-gray cobbly loam, slightly acid surface horizon about 7 cm thick. The next horizon is a very dark-gray cobbly clay loam of neutral pH which extends to a depth of about 25 cm. This is underlain by a grayish-brown cobbly clay about 40 cm thick, also neutral in pH. The next horizon is thin, only 7 cm thick, and is a mildly alkaline, very cobbly silty clay. A moderately alkaline, yellowish-brown, very cobbly clay loam about 18 cm thick comprises the next horizon. A very pale brown indurated layer is encountered at about 95 cm. Permeability is very slow, and potentials of runoff and erosion are moderate. Gribble soils are capable of supplying 15-20 cm of moisture over the growing season, and have an available water holding capacity of 5-13 cm of moisture. In a drought year, this site would be drier than the McCoin Orchard site. Rooting depth is 50-100 cm on this soil, and spring growth on Shubby Rolling Hills range sites, which include the Blanchard collection site, generally begins in late-March or early-April.

Historically, the climax plant community of this site was primarily composed of herbaceous species, with bluebunch wheatgrass the dominant. Idaho fescue and Sandberg's bluegrass were also common, and Thurber's needlegrass (Stipa thurberiana Piper) was also present. Perennial forbs, including yarrow, phlox (Phlox spp.), and lomatium (Lomatium spp.) also occurred. Perennial shrubs made up about 10% of the community, and included big sagebrush (Artemisia tridentata Nutt.), rabbitbrush, bitterbrush, and wax currant.
Western juniper cover has increased slightly on this site, and the perennial shrubs have been largely eliminated (table 2.6, table 2.7). Idaho fescue is the dominant perennial bunchgrass in the fence row refugium, and bluebunch wheatgrass contributes about half as much cover as does Idaho fescue. Cheatgrass cover is high at this site.

**Combs Flat** The Combs Flat Idaho fescue population occurs on a gently sloping, north facing upland. The soil at the Combs Flat site is a Lookout very stony loam, 0-40 % slopes (LvE), with inclusions of a Lookout loam, 2-6 % slopes (LoB). Idaho fescue is most abundant on the very stony loam. An exclosure (referred to as the study plot in table 10) was erected on the Lookout loam, and a field experiment was run in the exclosure.

A representative profile of the Lookout series has a neutral, brownish-gray, very stony loam surface horizon that extends to a depth of about 20 cm. Between the depths of 20 and 50 cm is a brown, very stony clay that is usually neutral or only slightly alkaline. A pale-brown indurated hardpan is encountered at depths of 50 to 75 cm, and is underlain by basaltic bedrock. The Lookout loam differs from the very stony loam in having a thicker surface horizon with few or no stones and a lower clay content in the subsurface horizons. Included in areas mapped as Lookout loam are inclusions having a sandy loam or fine sandy loam surface horizon. The diversity of soil textures described for this mapping unit compares favorably with what actually exits at the Combs Flat site. Permeability is slow, with the potential (depending on
slope) of high rates of surface runoff and soil erosion. The moisture-holding capacity of this series is low.

Historically, this site was dominated by perennial grasses. Bluebunch wheatgrass was the dominant herbaceous species, though Idaho fescue could be a co-dominant on north facing slopes. Sandberg’s bluegrass was common. Scattered juniper and sagebrush were present also.

Juniper cover on Combs Flat has increased, though sagebrush cover has likely changed little (table 2.6, table 2.7). Cover by native perennial bunchgrass has been greatly reduced, with Idaho fescue and bluebunch wheatgrass accounting for less than 1 % cover each. Sandberg’s bluegrass covers 6 % of the site. Cheatgrass has invaded the site and has higher cover (9 %) than any other grass.

**Island**  The population of Idaho fescue on the Island grows on an essentially flat, level mesa. Driscoll (1964) describes three soils for the Island, two of them supporting a *Juniperus/Artemisia/Agropyron* association and the third supporting a *Juniperus/Purshia/Agropyron* association. Idaho fescue seed was collected from the latter association. The soil beneath the *Juniperus/Purshia/Agropyron* association is a very shallow sandy loam lacking definite genetic horizons. This soil developed from aeolian parent materials and is slightly acid to neutral. Beneath the 20 cm thick sandy loam is a buried stony clay loam. The buried soil developed from the same alluvial material as the two soils underlying the *Juniperus/Artemisia/Agropyron* association, but contained many more stones. The A horizon of the buried solum is 35 % stones
by volume, and the B horizon is 80-90% stones. At its top, the buried soil is neutral, but alkalinity increases with depth. At a depth of 50 cm, a discontinuous indurated layer is encountered, and below the hardpan is fractured bedrock.

Available water capacity is low; 4.25 cm can be held between the depths of 5 and 35 cm. During drought, the Island is likely to have the driest soil of any of the five sites. Plants growing on this site extended their roots through both soils and into the underlying fractured bedrock (Driscoll 1964). Though the water holding capacity of these soils is low because of the high stone content, the soil texture allows deep infiltration. Plants able to explore the fractured bedrock have greater access to moisture than do plants growing on the soils beneath the Juniperus/Artemisia/Agropyron association.

Historically, the vegetation of the Island was similar to that which is present currently, with the exception of some introduced annuals, particularly cheatgrass (Driscoll 1964). The community was a mix of shrubs and grasses, with scattered juniper. Bluebunch wheatgrass was the most common perennial bunchgrass. Idaho fescue, Sandberg’s bluegrass, and Thurber’s needlegrass were well represented. Perennial forbs were also present, but contributed relatively little cover. Bitterbrush was the dominant shrub, but gray rabbitbrush (*Chrysothamnus nauseosus* (Pall.) Britt.) was present at low density.

Juniper is present on the Island currently, but did not appear in my transect. Sagebrush covers 2% of the site. Idaho fescue and bluebunch wheatgrass have cover values of 6% each. This was the only site which had a cryptogamic crust on the soil
Cheatgrass is present on the Island, but did not appear in any of the quadrats.

The Study Species

Idaho fescue  Idaho fescue is a native, cool-season, perennial bunchgrass, and is widely distributed in western North America from British Columbia to northern New Mexico. Across this region, Idaho fescue is generally found between the elevations of 250 and 3700 m in areas receiving 23 cm, or more, of annual precipitation (Roche 1983). In high seral rangeland communities on mesic sites, Idaho fescue is the dominant herbaceous species (Daubenmire 1970; Tisdale and Hironaka 1981; Doescher et al. 1986). Idaho fescue is an excellent forage for both wildlife and livestock, particularly late in the growing season and in winter (Vavra and Sneva 1978; Holechek et al. 1982; Dragt and Havstad 1987).

The leaves of Idaho fescue are filiform, between 5 and 12 cm long, involute, numerous, and densely clumped. Fine culms rise to a height of 30-100 cm, and support a panicle of numerous spiklets of 5 to 7 flowers. Reproduction is by seed, though vegetative growth of the bunchgrass and subsequent fragmentation gives rise to new individuals (clones) as well (Stubbendieck et al. 1992).

Idaho fescue is generally found on moderately deep, well-drained, loamy soils on all exposures (Roche 1983; Stubbendieck et al. 1992). In central Oregon, Idaho fescue is commonly found on north exposures. This grass has a fibrous root system,
with root density greatest in the upper 2 cm of the soil profile. Weaver (1982) found 66% of the root biomass of Idaho fescue within the top 4 cm of a soil. Fully 40% of root biomass occurred within the top 2 cm of the soil, with equal amounts in each centimeter. Root biomass averaged 725 g/m² in the top 10 cm of the soil profile.

Spence (1937) described Idaho fescue as having an average of 201 roots per individual which reached a mean depth of 40 cm.

Pitt and Wikeem (1990) described the phenology of Idaho fescue growing in British Columbia, where mean annual precipitation equals 296 mm and is rather uniformly distributed throughout the year. Vegetative growth was initiated in early April, and floral initiation followed in May. Flowers were fully developed by June, seed set and shatter occurred in July, and the grass had cured by the end of August. Fall regrowth was seen in September, October, and November. Idaho fescue is one of the earlier native perennial bunchgrasses to resume growth in the spring (Borman et al. 1991).

Observations suggest that seed production in Idaho fescue is directly related to the availability of soil moisture. Seed production appears to be stimulated by above-normal soil moisture availability during May and June (L. Eddleman, pers. comm.). Idaho fescue seed production in 1988 was good (L. Eddleman, pers. comm.) and spring precipitation was roughly normal (table 2.8). However, precipitation delivered during April was above the long-term mean, possibly compensating for sub-normal rainfall during May. Spring precipitation amounts were well above average in 1989, and seed production was high. Rainfall during May and June of 1989 was below the
long-term averages for these months, while more rain than usual fell in March and April. Seed set was poor in 1990, and the amount of precipitation received during the spring was below the long-term mean. Spring precipitation was near normal in 1991, and seed production was fair. April was a relatively dry month in 1991, but the other months of the spring growing season were wetter than usual. Above average quantities of precipitation during May and June, or very high precipitation early in the growing season, appear to promote seed production.

However, spring seed production by *Festuca scabrella* Torr. is largely controlled by floral initiation during the previous fall (Johnston and MacDonald 1967). Differentiation of floral primordia occurs in late August and early September, rather than in spring, and seed production is constrained by this autumn initiation of floral buds. Floral initiation by Idaho fescue may also occur in fall rather than spring, as this phenology is common among grasses having northerly distributions (Johnston and MacDonald 1967). Interestingly, years of good seed production alternated with years of poor seed set during Johnston and MacDonald’s study. The investigators found only a weak correlation between weather and floral initiation, but reported that spaced plantings and nursery conditions [favorable moisture/nutrient and temperature regimes] promoted the differentiation of floral primordia.

Roche (1983) characterizes Idaho fescue as a decreaser, as overuse has led to a decline in the density of Idaho fescue on abused rangelands. Driscoll (1964) compared a relict area to surrounding grazed lands and reported the virtual elimination of Idaho fescue and greatly reduced abundances of other native perennial
Table 2.8. Idaho fescue seed production and spring precipitation (mm), central Oregon, 1988-1991.

<table>
<thead>
<tr>
<th>Year &amp; Month</th>
<th>Station</th>
<th>Redmond</th>
<th>Prineville</th>
<th>Madras</th>
<th>Seed Set</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1988</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>6.35</td>
<td>15.49</td>
<td>14.22</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>29.72 (+18.03)</td>
<td>34.04 (+18.03)</td>
<td>37.08 (+21.08)</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>9.65 (-13.21)</td>
<td>17.78 (-10.16)</td>
<td>—</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>25.65 (+4.57)</td>
<td>17.02 (-9.40)</td>
<td>30.73 (+7.37)</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>71.37 (-0.52)</td>
<td>84.33 (-4.83)</td>
<td>—</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>41.91 (+25.65)</td>
<td>50.80 (+32.00)</td>
<td>51.56 (+32.26)</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>44.45 (+32.77)</td>
<td>65.29 (+49.28)</td>
<td>41.40 (+25.40)</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>13.46 (-9.40)</td>
<td>22.10 (-5.84)</td>
<td>17.53 (-6.35)</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>2.79 (-18.29)</td>
<td>5.84 (-20.57)</td>
<td>3.05 (-20.32)</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>102.61 (+30.73)</td>
<td>144.03 (+54.87)</td>
<td>113.54 (+30.99)</td>
<td>Good</td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>24.13 (+7.87)</td>
<td>24.13 (+5.33)</td>
<td>12.70 (-6.60)</td>
<td>Poor</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>10.92 (-0.76)</td>
<td>14.22 (-1.79)</td>
<td>10.41 (-5.59)</td>
<td>Poor</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>27.43 (+4.57)</td>
<td>27.84 (+0)</td>
<td>44.45 (+20.57)</td>
<td>Poor</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>2.03 (-19.05)</td>
<td>7.37 (-19.05)</td>
<td>3.56 (-19.81)</td>
<td>Poor</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>64.51 (-7.37)</td>
<td>73.66 (-15.51)</td>
<td>71.12 (-11.43)</td>
<td>Poor</td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>26.16 (+9.91)</td>
<td>30.48 (+11.68)</td>
<td>33.78 (+14.48)</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>4.83 (-6.86)</td>
<td>7.87 (-8.13)</td>
<td>10.16 (-9.14)</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>33.02 (+10.16)</td>
<td>40.89 (+12.95)</td>
<td>31.75 (+7.87)</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>28.96 (+7.87)</td>
<td>50.04 (+23.62)</td>
<td>—</td>
<td>Fair</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>92.97 (+21.08)</td>
<td>129.28 (+40.12)</td>
<td>—</td>
<td>Fair</td>
<td></td>
</tr>
</tbody>
</table>

1. Values in parentheses are deviations (mm) from the long-term average.  2. Missing data in this period.
grasses as a result of grazing. Poor livestock management and the introduction of alien annuals over the last 125 years have led to the conversion of sagebrush/steppe communities once dominated by perennial bunchgrasses to communities dominated by alien species (Piemeisel 1951; Hironaka and Tisdale 1963; Harris and Goebel 1976; Allen and Knight 1984). Forage production had dropped to 50 % or less of potential production on 88 % of sagebrush-grass rangelands (Anon. 1972). These degraded rangelands are often dominated by cheatgrass and brush species (Young et al. 1987; Evans and Young 1984; Harris 1967; Harris and Goebel 1976).

**Cheatgrass** Cheatgrass is a winter annual that was introduced to the United States about 1850 (Klemmedson and Smith 1964; Mack 1981). The alien is now found in grasslands and prairies throughout North America from sea level to 10,000 feet (Roche 1983; Stubbendieck et al. 1992). Cheatgrass achieves its greatest abundance on disturbed sites (e.g. heavily grazed rangeland, road sides, soil heaps, burned areas) where annual precipitation is between 20 and 50 cm. It has become a common constituent of sagebrush-steppe communities, and is often the dominant herbaceous species. During a brief period in the spring, cheatgrass is a fair to good forage, but becomes less suitable for livestock and wildlife when the inflorescence emerges (Stubbendieck et al. 1992). Senescence is induced in cheatgrass by moderate moisture stress (a predawn xylem pressure potential of about -0.8 MPa) (Link et al. 1990).
Phenotypic expression by cheatgrass is strongly influenced by environmental factors. Cheatgrass leaves are thin, flat, pubescent, and 5-12 cm long by 0.3-0.7 cm wide. Roots are moderately fine and poorly suberized, and root growth is strongly geotropic (Harris 1967). Cheatgrass is a bunchgrass having weak culms that are more or less erect and rise to 10-60 cm. Reproductive culms support a drooping, one-sided panicle. Depending upon the availability of soil resources, particularly moisture (Richardson et al. 1989), the panicle may contain from one to many spikelets, with 5-8 cleistogamous flowers per spikelet. The lemma carries a 1.2 to 1.8 cm long awn, which can cause eye, ear, and mouth injury to ungulates. Virtually every seed produced is viable, and is capable of germinating while still in the dough stage (Hulbert 1955). All viable seeds will germinate very rapidly given sufficient moisture for imbibition. If moisture is not available, dormancy may be induced by repeated freeze/thaw cycles (Young et al. 1969).

Link et al. (1990) described the phenology of cheatgrass growing in southeastern Washington. By mid-February, first leaves were fully expanded. Shoot growth continued slowly through early spring, with middle leaves fully expanded by late March. Floral buds appeared in mid-April and flowers were fully developed by early May. Mature seeds were present by mid-May, and seed shatter occurred late in the same month. Plants were dead or senescent by early June. Supplemental irrigation delayed phenological development by about 10 days.

Though plant growth is affected by many abiotic factors, the availability of soil moisture is the primary environmental factor influencing plant growth and
survival on Intermountain rangelands (Harris 1967; Harris and Goebel 1976; Young and Evans 1982). The ability of a plant to successfully compete for and extract soil moisture is a major determinant of the plant’s fitness (Eissenstat and Caldwell 1988), particularly on sites invaded by cheatgrass (Harris 1967; Melgoza et al. 1990).

Cheatgrass has a competitive advantage over native perennial grasses that is largely due to root phenology and morphology (Harris 1967, 1977; Harris and Wilson 1970). Cheatgrass germinates in the fall and produces roots that grow rapidly down into the soil profile, even at cool soil temperatures. Bluebunch wheatgrass (Agropyron spicatum (Pursh) Scribn.) is much less effective in occupying a soil, as root growth is considerably slower and essentially ceases when soil temperatures drop below 8 °C. Thus, cheatgrass seedlings are well positioned for rapid growth with the arrival of spring conditions, whereas seedlings of bluebunch wheatgrass must still produce the greater portion of their root system. Harris and Goebel (1976:17) stated, "It is a fair generalization to say that seedlings of annual grasses are more vigorous and faster growing than seedlings of perennial grasses in fall and winter." Like native perennial grasses, cheatgrass root density is greatest in the upper portion of the soil profile, but the alien also extends roots to depths in excess of a meter. Nearly three-quarters (470 g/m²) of cheatgrass root biomass is found in the upper 10 cm of the soil; only 2 % of root biomass is below depths of 40 cm but roots extend to 160 cm (Cline et al. 1977). Spence (1937) found cheatgrass to average seven roots per individual with an average rooting depth of 30 cm. For comparison, Spence (1937)
found Idaho fescue to root to 40 cm on average, and Harris (1967) reported an average depth of 95 cm for bluebunch wheatgrass roots.

Literature Cited


CHAPTER III. A REVIEW OF THE LITERATURE
Germination of a seed is stimulated by a favorable microenvironment, such as the availability of moisture for imbibition coinciding with temperatures favoring growth (Harper 1977; Young and Young 1986). Imbibition is the first step in the process of germination, and mature seeds must take up moisture before germination can occur (Copeland and McDonald 1985). Once imbibition has occurred, metabolic processes leading to germination are started. In some species, germination is not prevented by freezing temperatures and once imbibed, these seeds will germinate (e.g. Evans and Young 1982; Young and Evans 1982; Buman and Abernethy 1988). Other species will germinate if a freezing temperature alternates with a warmer one, such as 10 °C in the case of squirreltail (*Sitania hystrix* (Nutt.) J.G. Smith) (Young and Evans 1977) and cheatgrass (Mack and Pyke 1984; Thill et al. 1979).

In addition to the influences of a heterogeneous environment, germination may be regulated by seed dormancy, which will prevent germination despite favorable conditions (Harper 1977; Baskin and Baskin 1981; Young and Young 1986). In general, seeds are dormant when dispersed (Harper 1977). Simpson (1990:19) stated, “seed dormancy in grasses is general rather than exceptional.” Dormancy is an adaptive trait allowing an organism to escape or avoid drought, temperature stress, flooding, fire, and other hazards (Simpson 1990). Seed dormancy may be caused by many factors, including embryo immaturity at dispersal, inhibitory compounds in the seedcoat or endocarp, and structural barriers to moisture or gas uptake and cell

Seed dormancy is less common in the Graminae than in other temperate zone plant families. Grime et al. (1981) found the germinability of fresh seed to be greater in Poaceae than in Asteraceae, Fabaceae, Cyperaceae, and Apiaceae. Most grasses produce seed crops that are at least partially nondormant at maturity and capable of prompt germination at the time of seed shatter, or even earlier. However, germinability of grass seed varies substantially among species, and within populations of the same species, following seed maturation (Nelson and Wilson 1969; Shaidaee et al. 1969; Harper 1977; Benech Arnold et al. 1992). For example, seeds of Sandberg's bluegrass germinate poorly unless after-ripened for six months (Evans et al. 1977) whereas seeds of squirreltail are nondormant at dispersal (Young and Evans 1977); both these grasses are common on Intermountain rangelands. Additionally, dormancy can be induced in a nondormant seed by environmental conditions (Harper 1977; Baskin and Baskin 1981).

Water relations of the maternal plant strongly influence dormancy in seed progeny, with water stress during grain filling resulting in reduced dormancy (Benech Arnold et al. 1992; Nelson and Wilson 1969; Belderok 1961). Likewise, high temperatures during seed development reduce, and low temperatures increase, the level of dormancy in the seed (Simpson 1990). Young and Evans (1977) reported variation in the germination response to temperature of squirreltail seeds collected in different years from natural populations subject to ambient weather conditions, but did
not identify the causes. Germinability of grass seed generally increases over the first
year or two following seed production as after-ripening occurs and dormancy is
broken (Rice 1989; Grime et al. 1981; Evans et al. 1977; Shaidaee et al. 1969). The
term after-ripening is used to refer to the often poorly understood “...interaction
between seed and environment, taking place over time, that leads to the loss of
dormancy” (Simpson 1990:46). After-ripening requirements of Idaho fescue, or
changes in germinability through time following seed shatter, are not reported in the
literature.

Seed dormancy can influence the outcome of competitive interactions among
plant populations (Simpson 1990). Asynchronous germination of competing plant
species confers an advantage to the earlier-germinating species. All else being equal,
the plant which initiates growth earliest will have the greatest success in sequestering
limited resources, thereby diminishing the success of competitors (Harper and Ross
particular, to germinate more rapidly, on average, than did sedges, shrubs, and trees;
annual forbs had germination rates comparable to perennial grasses.

Seed germination is promoted by light in many species (Grime et al. 1981). In
some very small-seeded species, the best example being lettuce (Lactuca sativa L.),
germination will not occur without exposure to light. However, the seeds of most
grasses, which are in the intermediate size classes, germinate readily in darkness
(Toole 1976; Grime et al. 1981; Young et al. 1981; Thill et al. 1984; Doescher et al.
1985).
In environments characterized by the unpredictability of periods favorable for germination and growth, dormancy in plants tends to be opportunistic, and is induced, enforced, and broken by environmental stimuli (Harper 1977). In arid and semi-arid environments, where precipitation is highly unpredictable, water plays an important, if not paramount, role in breaking dormancy (Harper 1977). Winter annuals of the Mojave and Chihuahuan deserts, for example, will not germinate until sufficient precipitation (10-15 mm) has fallen (Barbour et al. 1987). It is thought that less precipitation is insufficient to leach inhibitory compounds from the seedcoat.

Evans and Etherington (1990) investigated the relationships between germination and water stress in 15 species found in diverse habitats and found four general patterns. Most commonly, the extent of seed germination progressively decreased as water stress increased; this response was exhibited by most of the species studied regardless of habitat type. Species commonly occurring in marshes had their seed germination strongly inhibited by all levels of moisture stress below -0.05 MPa. At the other extreme, a ruderal species was entirely insensitive to water stresses ranging -0.05 to -1.5 MPa, and achieved 100% germination in all treatments. Some species which occur in dry or droughty habitats were insensitive to all but the greatest water stress (-1.5 MPa). For all species except the ruderal, the rate of germination also declined with increasing water stress (though not always linearly). The rate of germination of the ruderal’s seeds did not change over the range of water stresses tested. On semiarid rangelands, the availability of moisture for imbibition is the pre-eminent factor affecting seed germination (Young and Evans 1982; Jordan
In rangeland grasses, sufficient moisture to allow imbibition will usually stimulate germination. Harris (1977) held that rapid germination at low water potentials is advantageous in rangelands.

For most species, seed germination is markedly influenced by temperature. Germination is often prevented by extreme temperatures and the most rapid and extensive germination occurs at an optimal temperature. Extreme and optimal temperatures, determined by germinating seeds under favorable moisture conditions, are referred to as cardinal temperatures (Thompson 1970; Garcia-Huidobro et al. 1982a, b). The base temperature ($T_b$) is the temperature below which no seeds germinate, and the upper limit is called the maximum temperature ($T_m$). The optimum temperature ($T_o$) is usually defined as the temperature at which the rate of germination is greatest. The $T_o$ is not defined on the basis of germination percentages as total germination is often very similar over a range of temperatures near the optimum (fig. 3.1). Two additional cardinal points, $T_v$ and $T_{v'}$, define the inflection points that bound the range of near optimal temperatures. Of many species studied, Grime et al. (1981) found grasses, legumes, and composites to be the least sensitive to temperature. Seeds from these plant families tended to germinate well over a broad range of constant temperatures. Conflicting reports of optimal and limiting temperatures for a particular species suggest ecotypic differences. Not only do cardinal temperatures vary among ecotypes, they can also change with seed age (Thill et al. 1984; Hulbert 1955). Additionally, the effects of moisture and temperature on
Figure 3.1 Cardinal temperatures in cheatgrass. a) Predicted germination at 0 MPa. b) Median response (50% germination) times at different temperatures and water potentials. From Buman and Abernathy 1988, Thill et al. 1979, & Hulbert 1955.
seed germination are usually interdependent (Thill et al. 1979; Doescher 1983; Doescher et al. 1985).

The seeds of many herbaceous species attain better germination under fluctuating temperatures than under constant temperatures (Thompson and Grime 1983; Thompson et al. 1977). In some cases, seeds that germinate under fluctuating temperatures do not germinate when temperatures are held constant. Seeds of many species, particularly ruderals, which germinate at constant temperatures given light, do not germinate in darkness unless temperature fluctuations are greater than 4 °C. These responses were interpreted as mechanisms which prevented germination beneath other plant canopies and their litter, or from depths too great for successful seedling emergence. Generally, fluctuating temperatures promote germination, and greater fluctuations are required when seeds are germinated in darkness compared to germination under lights. However, many of the grasses, including sheep fescue (*Festuca ovina* L.), are insensitive to both light and temperature fluctuations.

Ghersa et al. (1992) showed that sensitivity to the amplitude of diurnal temperature fluctuations strongly influenced the germination of Johnsongrass (*Sorghum halepense* L.) seed. In the field, where temperature fluctuations were highly dependent upon depth, seed germination declined with increasing depth of burial. When soil columns were incubated at alternating temperatures having an amplitude of 10 °C, seed germination was independent of depth. Incubation at constant temperatures inhibited seed germination, regardless of depth of burial. Sensitivity to temperature fluctuations decreased with after-ripening, particularly when
stored at room temperature, a trend reported by other researchers also (Thompson and Grime 1983).

The depth from which a seedling can emerge to the soil surface is influenced by seed size. The larger the seed, the greater the depth from which successful seedling emergence can occur (Jurado and Westoby 1992). Thompson and Grime (1983) found small seed size to be correlated with a requirement for light and/or large temperature fluctuations, as would occur at or near the soil surface, for germination. Larger seed size was correlated with the capacity for germination in darkness and at constant temperatures. Though greater burial depths may reduce the risk of seedling desiccation, the probability of burial declines with increasing seed size (Harper et al. 1965; Mortimer 1974 cited in Thompson and Grime 1983; Jurado and Westoby 1992). Small seeds are more likely to fit into the depressions and fissures in a soil surface than are large seeds. Seed germination is often enhanced by burial in soil or litter (Evans et al. 1977; Young and Evans 1977).

Seed size has little effect on germinability of native grasses, though larger seeds within a seed lot are likely to give more vigorous seedlings (Kneebone and Cremer 1955). Large-seeded native grasses do not tend to produce more vigorous seedlings than small-seeded species, on the whole. However, within a species, larger seeds tend to produce seedlings that emerge earlier and grow faster than do seedlings arising from small seeds. Additionally, size and longevity of seeds, both within and between seed lots, do not appear to be correlated in rangeland plants (Hull 1973).
In wild radish (*Raphanus raphasistrum* L.), however, the relative growth rates of seedlings are independent of seed mass (Choe et al. 1988). Shipley and Peters (1990) examined a large data set including diverse species and found only a weak negative relationship between seed size and the relative growth rates of seedlings. In the Australian arid zone flora, seedlings of large-seeded species tended to have lower relative growth rates than did seedlings of small-seeded species (Jurado and Westoby 1992). (The Australian arid-zone seedlings were grown individually, without competitors.) Initial seed reserves had the greatest influence on seedling mass during the first ten days of growth. The rapidity with which germination commenced and relative growth rate were less influential factors. Under field conditions, where a seedling faces competition from other seedlings, the speed of germination assumes greater importance (Harper and Ross 1972; Weiner 1985). Allocation patterns in seedlings of large- and small-seeded species do not differ (Choe et al. 1988; Jurado and Westoby 1992).

Within two years of production, seed viability in perennial grasses normally changes little, and viability generally remains high (80% germination) through 4 or 5 years (Hull 1973). Viability does diminish with time, and is often greatly reduced within 10 years (Hull 1973; Tisdale 1959). For example, ‘Nordan’ crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Shultes) seed attained 86% germination in the year it was produced, but only 11% after 14 years of storage in an unheated shed (Hull 1973). Cleaned seeds, from which the glumes, lemma, and palea have been wholly or partially removed, lose viability during storage much more
rapidly than do unthreshed seeds (Justice and Bass 1978). Benech Arnold et al. (1992) found the glumes of Johnsongrass to enforce seed dormancy and suggested the glumes prevented oxygen diffusion to the enclosed caryopsis (leachate from glumes did not inhibit germination). Respiration rates were higher and increased more rapidly in seeds from which glumes had been removed compared to intact seeds. Seed viability and germinability is better preserved if unthreshed seeds are stored in a cool, dry environment. Harrington (1972) suggested that seed longevity is doubled with each 5 °C reduction in seed temperature and each 1% reduction in seed moisture content.

Adaptation to the rangeland environment is related to physiological and phenological traits of seed dispersal, dormancy, after-ripening, and germination. For example, rubber rabbitbrush seeds collected from sites having mild winters and relatively low risks of winter and spring frosts germinated more rapidly at 3 °C than did seeds of the same species collected from sites where the risks of winter and spring frosts were high (McArthur et al. 1987). Frost and drought are the major threats to the survival of rangeland plant seedlings (Mack and Pyke 1984; McArthur et al. 1987). In central Oregon, temperatures below freezing are possible in any month of the year, and the delivery of precipitation is unpredictable. Thus, seedling survival in central Oregon is reduced by drought, freezing temperatures, and physical up-rooting during frost heaving.
Germination of Idaho Fescue Seed  Young et al. (1981) tested six accessions of Idaho fescue for seed germinability at 55 constant and alternating temperature regimes, which included temperatures from 0 to 40 °C and 8 hour warm/16 hour cold periods with no light. Temperature regimes between 15 and 25 °C supported optimum germination (defined as those regimes which produced germination percentages that were within the 99 % confidence interval of the highest mean germination percentage). The authors obtained maximums of 68-81 % germination in the most favorable regimes and 34-47 % mean germination across all temperature regimes tested. Of the six accessions, five were breeding lines and one was wild. The wild accession gave the lowest germination when averaged across all temperature regimes. However, in the seven regimes which the authors considered optimal, the wild accession averaged 77 % germination, which was higher than any of the breeding lines averaged. Though total germination was often low, Idaho fescue seed germinated over a wide range of temperature. Eighty-seven percent of the tested regimes induced some germination in the wild accession, and seed from the breeding lines germinated in 90-98 % of the tested temperatures. None of the temperature combinations stimulated 90 % or better germination in any Idaho fescue accession. Over half the regimes tested supported 50 % or less germination. Because of this, and despite germination in 98 % of the temperature regimes tested, Young and Evans (1982) considered the germinability of Idaho fescue to be poor. Compared to numerous species from the Agropyron, Elymus, Festuca, Poa, and Bromus genera,
Idaho fescue fell into the bottom five germinability classes (fair to very low) on a twelve class scale.

Tisdale (1959) reported 50-95% germination in 21 days among Idaho fescue seeds collected from 18 sites in British Columbia and the western United States. In the material examined by Tisdale, most (55-90%) florets were empty. Of the five to seven florets per spikelet, usually three or fewer produced a filled seed. Seeds that had been harvested 11 and 12 years earlier did not germinate (storage conditions were not described).

Doescher et al. (1985), using normally-developed filled seed, obtained much higher germination percentages than did Young et al. (1981). For Idaho fescue seed from sagebrush-grass communities, germination ranged from 62 to 97% at constant temperatures between 5 and 30°C in dark conditions. Within the range of 10 to 25°C, germination averaged 90%. Mean germination was 71% at 5°C. The rate of germination was greatest at 20 to 25°C, and declined as temperature decreased or increased beyond the optimum range. Eight month old seed germinated at optimum temperatures required only 6.6 days to achieve 50% germination (Doescher 1983). At 10 and 30°C, the germination rate was half that seen at optimum temperatures; germination was five times slower at 5°C (Doescher 1983). Additionally, Idaho fescue from sagebrush-grass communities germinated well over a range of moisture stress (Doescher et al. 1985). At temperatures of 15 and 20°C and water potentials of 0, -0.6, and -0.9 MPa, germination ranged between 52 and 95%, and averaged 85
The rate of germination declined as moisture stress increased, with the greatest decrease at the highest temperature and greatest moisture stress.

Despite the work of Young et al. (1981) and Doescher et al. (1985), the cardinal temperatures of Idaho fescue remain undetermined. Table 3.1 summarizes the results obtained by these researchers for constant temperatures. The base temperature ($T_b$) remains unknown, but it is less than $0 \, ^\circ C$. The maximum temperature may be $40 \, ^\circ C$, but could be lower. The optimum temperature appears to be $20 \, ^\circ C$ (table 3.2), but the rate of germination was the same at $25 \, ^\circ C$ at 0.0 MPa. The optimum may lie between 20 and $25 \, ^\circ C$. As moisture stress increases, the optimum temperature falls. The near-optimum range appears to be bound by $10 \, ^\circ C$ ($T_{n}$) and $25 \, ^\circ C$ ($T_{m}$). Germination is slowed at $10 \, ^\circ C$, however. Germination is swift at $30 \, ^\circ C$, but few seeds germinate. The range of temperatures tested is too limited and too coarse to allow cardinal points to be determined with precision, and these values vary with the availability of moisture and are likely to vary with ecotype.

Total germination and rate of germination of Idaho fescue seed is a function of both temperature and water stress. Doescher (1983) found the interaction of temperature and water stress to affect both the rate and extent of Idaho fescue seed germination significantly (significance level of 0.05). Thus, the value of cardinal temperatures will depend upon the level of water stress. Any model of Idaho fescue seed germination would need to include both temperature and water potential.

Having found Idaho fescue seeds from sagebrush-grass communities to germinate over a broad range of temperature and moisture conditions, Doescher et al.
Table 3.1 Empirical and predicted germination (%) of Idaho fescue seed at constant temperatures.

<table>
<thead>
<tr>
<th>Investigators</th>
<th>Temperature (C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Young et al. 1981</td>
<td>18</td>
</tr>
<tr>
<td>Young &amp; Evans 1982</td>
<td>20</td>
</tr>
<tr>
<td>Doescher et al. 1985</td>
<td>---</td>
</tr>
</tbody>
</table>

1. Predicted germination using a quadratic response surface.

Table 3.2 Median response times (days) for Idaho fescue seed germinated over a range of temperature and water stress. From Doescher (1983).

<table>
<thead>
<tr>
<th>Ψ (MPa)</th>
<th>Temperature (C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>0.0</td>
<td>25</td>
</tr>
<tr>
<td>-0.6</td>
<td>---</td>
</tr>
<tr>
<td>-0.9</td>
<td>---</td>
</tr>
</tbody>
</table>

(1985) noted the potential for ecologically significant recruitment of Idaho fescue during autumn. Germination and establishment of Idaho fescue during this period may reduce the competitive advantage of cheatgrass arising from its germination in the fall, as both species would begin occupying belowground space at the same time.

Germination of Cheatgrass Seed As an annual, cheatgrass is dependent upon seed production, dispersal, germination, and establishment for its continued existence.
Cheatgrass allocation to reproduction is high, as is typical for annuals, and shows many adaptations to better the chances of successful reproduction and re-establishment. Cheatgrass seed has an astounding ability to osmotically adjust water potential and establish gradients for moisture flow to the seed. McDonough (1975) studied the water relations of germinating cheatgrass seeds and found that within 40 hours of initiating imbibition, the water potential of cheatgrass seeds dropped to -1.0 MPa. After 60 hours, cheatgrass seed water potential dropped still further to -1.65 MPa, and remained at this low value for the duration of the 120 hour experiment. Cheatgrass seed is also viable while still in the dough stage, well before seed maturity (Hulbert 1955).

Cheatgrass seed can remain viable for at least 10 years if moisture content remains low (Hull 1973). Of 11 species of grasses and forbs studied by McDonough (1975), cheatgrass had the most rapid germination. Even after 10 years of storage, cheatgrass was among the most rapidly emerging species of the 40 grass, forb, legume, and shrub species, native and introduced, tested by Hull (1973). The seeds had been stored in unheated tin sheds in paper sacks, which were packed inside wooden "mouse proof" but not air tight containers. However, threshing cheatgrass seeds to remove awns can significantly reduce seed viability. Hulbert (1955) found that threshing killed or otherwise damaged 33-50 % of the embryos of processed seed, which was not detected until subsequent germination tests.

Once conditions allowing germination are established, cheatgrass seeds germinate very rapidly. Young et al. (1969) obtained 95 % germination with freshly
collected cheatgrass seed within two weeks under favorable conditions. Thill et al. (1979) found the current year's seed crop to require only 1 day to achieve 50% emergence under favorable conditions. Thus, cheatgrass seed will germinate once precipitation has been sufficient to allow imbibition, usually in the fall. Though fall tends to be a 'wet' time of year on Oregon rangelands, drought is common and many cheatgrass seedlings desiccate and die (Mack and Pyke 1984). Newly germinated seedlings may avoid death during drought if root length is less than 15 mm and the plumule has not elongated (Hulbert 1955). At this stage of development, the seedling is able to suspend germination (become quiescent); germination is resumed when water relations improve. Dormancy in cheatgrass seed can be induced by environmental conditions. After exposure to a winter of alternating freeze/thaw temperatures, the response of cheatgrass seed switched from simultaneous (all seeds germinating concurrently) to continuous germination, with seeds germinating at a slow rate over a twelve week period (Young et al. 1969). Light inhibits germination of fresh cheatgrass seed, which would act to prevent germination until burial (Hulbert 1955), but the inhibitory effect of light disappears with about two months of after-ripening.

Young and Evans (1982), using seed collected from four sagebrush-grass communities in central Nevada, found cheatgrass to germinate in all 55 constant and alternating temperature regimes tested (0 to 40 °C, see above). Mean germination across all temperature regimes was 81%. Maximum germination in the four accessions ranged from 94-100%. Roughly one quarter of the tested regimes proved
to be optimal, with an average of 96 % germination, and included regimes ranging from 2/25 (16 hours/8 hours) to 15/35 °C. Fully 75 % of the temperature regimes allowed greater than 75 % germination. A quadratic response surface developed from the above results predicts 26 and 13 % germination at constant temperatures of 0 and 40 °C, respectively, with considerably higher germination at intervening temperatures (table 3.3). Because of high germination across a broad range of constant and alternating temperatures, Young and Evans (1982) placed cheatgrass in the top two of twelve germinability classes.

Table 3.3 Predicted germination of cheatgrass seed at constant temperatures.

<table>
<thead>
<tr>
<th>Origin</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-5</td>
</tr>
<tr>
<td>Nevada¹</td>
<td></td>
</tr>
<tr>
<td></td>
<td>--</td>
</tr>
<tr>
<td>Oregon²</td>
<td></td>
</tr>
<tr>
<td>Washington²</td>
<td></td>
</tr>
</tbody>
</table>

1. Quadratic response surface (Young and Evans 1982)  2. Bivariate spline model (Buman and Abernathy 1988)

Other investigators have not attained the high germination percentages for cheatgrass seed reported by Young and Evans (1982). Cheatgrass seed collected in eastern Oregon and eastern Washington gave maximums of 67 and 93 % germination across a range of temperatures spanning -5 to 28 °C, and averaged only 40 and 53 % over all temperature regimes (Buman and Abernathy 1988). Still, seeds germinated in 90 % of the regimes tested. Optimum temperature regimes for Oregon cheatgrass
seed germination ranged from 0/30 (8 hours/16 hours) to 30/20 °C, but only 0/30 and 5/30 °C proved optimal for seed from Washington. Buman and Abernethy (1988) found a bivariate spline model to best fit the germination response of cheatgrass to temperature (table 3.3). Their model predicts cheatgrass germination in temperature regimes ranging from -5/5 to 30/30 °C. Predicted germination ranged between 60 and 67 % across all regimes within the optimum temperature range of Oregon cheatgrass and 86-93 % for the accession from Washington. Cheatgrass seed from Juniper Lake (Oregon) achieved optimum germination in more temperature regimes than did any other seed lot tested. At temperatures below 5 °C, however, germination of Oregon cheatgrass was suppressed.

Cheatgrass seed collected in eastern Washington germinated at constant temperatures of 10, 15, and 20 °C averaged 57, 71, and 68 % germination, respectively, when soil matric potential equalled 0.0 MPa (Thill et al. 1979). Both the extent and rate of germination decreased with increasing water stress (table 3.4). Germination was strongly inhibited when matric potential dropped below -1.0 MPa. An interaction between temperature and water stress is revealed in the table: germination is more rapid and extensive at the warmer temperature when water stress is low to moderate, but when water stress is high, low temperatures give better germination.

As the interaction between temperature and water stress suggests, cardinal temperatures are not constant, but vary with water potential. Additionally, cardinal temperatures differ among ecotypes. Though smaller intervals between germination
Table 3.4 Germination of cheatgrass seed over a range of constant temperatures (C) and at four levels of water stress (MPa)\(^1\).

<table>
<thead>
<tr>
<th>Temperature</th>
<th>Germination (%)</th>
<th>Median Response Time (Days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\Psi) 0</td>
<td>-0.3</td>
</tr>
<tr>
<td>10</td>
<td>57</td>
<td>55</td>
</tr>
<tr>
<td>15</td>
<td>71</td>
<td>52</td>
</tr>
<tr>
<td>20</td>
<td>68</td>
<td>57</td>
</tr>
</tbody>
</table>

\(^1\) From Thill et al. 1979

Temperatures would allow much greater precision, approximate cardinal points are apparent. At 0.0 MPa, the optimum temperature for cheatgrass seed germination is near 20 °C, and the optimum range is probably bounded by 15 and 25 °C. Temperatures of 10 and 30 °C appear to be outside the optimum range at 0.0 MPa. Harris (1967) found 20 °C to be the optimal temperature for cheatgrass seed germination, regardless of the level of water stress. Optimum temperature also varies with seed age: a temperature of 10 °C was optimum for fresh seed, 15 °C proved optimal for seed that had after-ripened for one month, and seed that was two or more months old germinated best at 20 °C (Hulbert 1955). In five month old seed, median response times were 7.9, 4.9, 3.2, and 3.7 days at temperatures of 10, 15, 20, and 25 °C (Hulbert 1955). The base temperature is between 0 and -5 °C, and the maximum temperature is likely between 40 and 45 °C. At other levels of water potential, the cardinal temperatures may be different, and are certainly different under conditions of high water stress.
On the scale of the individual seed, the soil surface is an extremely heterogeneous environment, offering a range of conditions for germination (Harper et al. 1965; Harper 1977). As a result, soil surface heterogeneity strongly influences the abundance and distribution of seedlings. Harper (1977:111) stated, "The presence or absence and the density of a seedling population depends not only on the availability of seed but on the frequency of 'safe sites' that provide the precise conditions required by a particular seed." He defined a safe site as a space that provides: 1) the stimuli to break seed dormancy; 2) the conditions and resources (e.g. water and oxygen) required for germination; and 3) some measure of protection from predators, pathogens and competitors. The lack of safe sites may preclude a species from a site, despite the presence of a seed source (Harper 1977).

Sterling et al. (1984) found soil surface microtopography to strongly influence seedling distributions in Mediterranean grasslands during secondary succession. The authors found a strong tendency ($\chi^2 > 8.26, p < 0.005$) for nutrient demanding species to occur in the bottoms of furrows in abandoned fields, whereas the tops of furrows were colonized by species more tolerant of water and nutrient stress. In rangeland communities, soil surface microtopography (5-100 mm) plays an important role in moisture retention by inhibiting runoff (Sanchez and Wood 1987; Mooers 1989). This microtopography also affects seed dispersal, germination and seedling establishment (Evans and Young 1970, 1972a, 1984). Depressions in the soil surface
tend to catch wind dispersed seed, moderate microclimate (both temperature and moisture), and provide conditions that favor seed burial (Evans and Young 1972b, 1984; Harper 1977). Accumulations of plant litter can have similar effects (Evans and Young 1970; Harris and Goebel 1976; Harper 1977).

It is likely that a critical feature of safe sites in rangeland communities is a microenvironment wherein moisture may be absorbed by a seed faster than it is lost to the atmosphere (Young et al. 1969). Evans and Young (1970) showed that plant litter reduced diurnal temperature fluctuations and maintained a higher relative humidity at the soil surface as compared to bare soil. The insulating effect of litter raised minimum temperatures to a range more favorable for germination, and prevented relative humidity from dropping below 60% over the course of a day. In contrast, temperatures on a bare soil surface dropped to near freezing, and relative humidity dropped to less than 20%. Mooers (1988) found more crested wheatgrass (*Agropyron cristatum* (L.) Gaertner) seedlings in plant litter than expected, and concluded that litter provides conditions required by the species for germination and establishment. Harris and Goebel (1976:2) held that, "except under unusually favorable conditions, some degree of seed covering is essential" for germination of the seeds of many rangeland species under natural conditions, including bluebunch wheatgrass, cheatgrass, and medusahead (*Taeniatherum asperum* (Simonkai) Nevski).

Soil microtopography can also increase the amount of seed surface area in contact with soil, and hence increase the amount of soil moisture available for imbibition and the efficiency of water absorption (Harper 1977). The degree of soil-
seed contact is also strongly influenced by seed morphology. For example, Harper et al. (1965) found the straight-awned, large seed of ripgut brome (*Bromus rigidus* Roth) to germinate better on a smooth soil surface. On rough surfaces, the seed tended to become suspended between soil clods. In contrast, the smaller seed of foxtail brome (*B. rubens* L.), with a curved awn, did better on rougher soils where the seed tended to fall between and conform to soil clods. Eckert et al. (1986) found soil surface heterogeneity to influence the emergence and distribution of seedlings on Wyoming big sagebrush (*Atemisia tridentata* ssp. *wyomingensis* Beetle & Young)-Thurber needlegrass sites. Perennial grasses most successfully established on litter and moss covered microsites, and from trench-like cracks in the surface of frost-heaved soils. Crusted, exposed soil surfaces generally did not provide safe sites for seeds of rangeland plants. The texture of exposed soil and the presence and particle size distribution of gravel on the soil surface influences the germination, emergence and distribution of both mountain (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) and basin big sagebrush (*A. tridentata* ssp. *tridentata* Nutt.) (Young et al. 1990).

In natural systems, most seeds germinate on the soil surface rather than from some depth (Harper 1977). Smaller seeds tend to be more successful in germinating and establishing on the soil surface, as larger seeds have a greater surface area exposed to the relatively dry atmosphere, as do seeds with rough surfaces (Harper 1977). Additionally, as seed size decreases, the relative heterogeneity of soil surface increases. Idaho fescue seeds are roughly half the size of cheatgrass seeds, and lack the sizable (1 to 2 cm long) awns of the latter species. Because of the large amount
of bare ground in rangeland communities coupled with frost-heaving, seed burial may be more frequent in semiarid rangelands than in more mesic grasslands with greater plant cover.

Safe Site Requirements of Idaho Fescue The literature contains scant reference to safe site requirements of Idaho fescue. However, the findings of Eckert et al. (1986) regarding the establishment of perennial grasses in litter accumulations probably apply to Idaho fescue: moss and litter covered microsites and cracks in the soil surface offer favorable sites for germination of perennial grass seeds. In the field, Idaho fescue appears to germinate in and emerge from litter, cracks in the soil surface, and beneath shrub canopies (P. Doescher and L. Eddleman, pers. comm.). Wasser (1982) recommended planting Idaho fescue seed at depths of ½" for best results when revegetating disturbed or degraded sites.

Safe Site Requirements of Cheatgrass Germination and establishment of cheatgrass is greatly aided by accumulations of plant litter and by cracks and depressions in the soil surface; smooth, bare soil generally does not provide safe sites for this species (Evans and Young 1970, 1972b). Evans and Young (1970) found the density of cheatgrass seedlings growing through litter to be four times that found on bare soil, and seedling distribution was strongly correlated with either litter or favorable microtopography. In a subsequent experiment, the same investigators (Evans and Young 1972b) found cheatgrass to germinate well during the fall in litter-
free microsites so long as the seed was either buried or in a pit in the soil surface.

Germination was best when seeds were buried in the bottoms of such pits, but when seeds were placed on a smooth, litter-free soil, germination was very poor.

Secondary succession in rangeland plant communities generally features an initial stage where introduced annual species (e.g. Russian thistle (*Salsola iberica* Sennen & Pau), tumble mustard (*Sisymbrium altissimum* L.), pepperweed (*Lepidium perfoliatum* L.) dominate the community (Piemeisel 1951; Hironaka and Tisdale 1963; Allen and Knight 1984). Cheatgrass usually does not become a significant component of these communities until litter from these herbaceous species has accumulated (Piemeisel 1951; Young et al. 1972; Evans and Young 1984).

**Seed Banks**

Generally seeds are dormant when dispersed, and the number of dormant propagules on a site is commonly several orders of magnitude greater than the number of growing plants (Harper 1977). Such a reserve of dormant seeds constitutes the seed bank, which includes both truly dormant seeds and those in which dormancy is enforced by environmental conditions (Harper 1977). Relatively little is known of the dynamics of recruitment from the seed bank in natural communities (Harper 1977). Harper (1977), citing the few studies that had been done (e.g., Donald 1959), noted that age structures in seed banks appear to be dominated by young seed recently
added to the reserve. Older seed cohorts are progressively less well represented in the store.

The size of the seed bank varies with community type and species. Species which do not germinate in darkness tend to form persistent seedbanks, whereas species lacking a light requirement for germination (which includes most grasses) are usually transiently or poorly represented (Grime et al. 1981). Harper (1977) cited a number of studies of the seed bank of perennial grasslands (e.g. Lippert and Hopkins 1950) and described a reserve of between 280 and 15000 seeds/m². In comparison, Major and Pyott (1966) found a reserve of 6000 to 12000 seeds/m² beneath an annual grassland in California, the higher seed densities occurring in areas subject to grazing. Seed stores in arable soils may attain a density of 86000 seeds/m² (Roberts and Stokes 1966).

Grasses, particularly perennial grasses, are often poorly represented in the seed pool (Harper 1977; Hassan and West 1986; Rice 1989). This is largely a reflection of the relative magnitudes of yearly seed production in annual and perennial grasses. Additionally, if reproduction is primarily vegetative, as is seen in some perennial grasses, seed production will be limited and the species largely absent from the seed bank (Rice 1989). Many of the native, late seral, perennial grasses of Intermountain rangelands tend to produce few seed (Wasser 1982; West 1988; Pyke 1990) and can, therefore, be expected to be poorly represented in the seed bank.

In natural grasslands, the seed bank is largely limited to the upper 2.5 cm of the soil profile and litter layer (Harper 1977; Major and Pyott 1966; Marlette and
Anderson 1986; Koniak and Everett 1982). Young and Evans (1975) found between 81 % and 91 % of the cheatgrass seed pool in the litter layer in a sagebrush-grass community. Fully 95 % to 97 % of the pool of germinable cheatgrass seeds was in the top 2.5 cm of the soil profile plus the litter layer. The seeds of other species (e.g. six-weeks fescue (Vulpia octoflora (Walt.) Rydb.), tumble mustard) were distributed similarly.

Seedling densities in soil samples from native sagebrush-grassland and adjacent crested wheatgrass seedings ranged from 264 to more than 5000 seedlings/m² (Marlette and Anderson 1986). At these sites, the seed bank was dominated by perennial species (big sagebrush, squirreltail, and crested wheatgrass). In contrast, the seed bank of a site that had burned 13 years earlier and been aerially seeded with a mixture of introduced wheatgrasses (crested and intermediate (A.intermedium (Host) Beauv.) wheatgrasses) was dominated by annual species, including broom buckwheat (Eriogonum vimineum Dougl.), cheatgrass, tumble mustard, and Cryptantha species (Koniak and Everett 1982). The only perennial grasses represented in the seed bank of the burned site was Sandberg’s bluegrass. Though no sagebrush grew on the burn, a few sagebrush seeds occurred in the seed bank. Seed density remained constant (1720-1906 seedlings/m²) over the burn, regardless of microsite (duff, transition, interspace). Cheatgrass seed densities of 4000 to 10,000 seeds/m² of soil are common once the alien has become well established on a site (Harris and Goebel 1976).

The density of seeds in the soil in sagebrush-grass systems is greater beneath shrub canopies than in interspaces, reflecting seed dispersal patterns and the trapping
of wind blown debris by shrubs (Young and Evans 1975; Koniak and Everett 1982; West and Hassan 1986). Young and Evans (1975) found between two and five times as many seeds beneath sagebrush canopies as in interspaces. Seeds were concentrated in the litter layer beneath canopies, but in interspaces, seeds were most commonly on the soil surface.

The correlation between above- and belowground floras tends to be weak in grasslands, though it varies with grassland type (Rice 1989; Coffin and Lauenroth 1989; Harper 1977). Weedy species usually dominate the seed banks of grasslands (Rice 1989; Young and Evans 1975; Koniak and Everett 1982). Hassan and West (1986) found 50% of the seed pool on a Wyoming big sagebrush site to be composed of cheatgrass seed, even though cheatgrass accounted for only 17% of the plant cover. Dominance of the seed pool by cheatgrass increased by a factor of two following a wildfire. In contrast, Marlette and Anderson (1986) found the seed bank in both crested wheatgrass stands and adjacent native vegetation to be dominated by the species that were dominant in the vegetation, though seeds tended to be clumped beneath their maternal plant.

The rate at which a seed bank is depleted varies with both functional group and species. The seed pools of horticultural weeds decline by about 50% per year if new seed additions are prevented; annual mortality is generally lesser in other species (Harper 1977; Rice 1989). Rice (1989) noted that microenvironmental heterogeneity and seed genetics appear to play a significant role in the depletion of seed banks. The presence of many annual species in rangeland communities results in dramatic
changes in the size of the seed bank through the seasons (Coffin and Lauenroth 1989; Young and Evans 1975). Spring seed production and fall germination by annuals generates large seed banks during the summer, and low densities in the fall. The large pool of cheatgrass seed present in late summer is essentially depleted by the following spring, primarily because of germination that starts with autumn precipitation, with some loss to predators and pathogens (Young and Evans 1975). As a result of germination, the pool of cheatgrass seed is low in the spring. Seed predation by ants, birds, and fungi, and grazing of seedlings by rabbits, rodents, and insects limits the reproductive success (and rate of seed addition to the seed pool) of many semi-arid and arid land plants (Bainbridge and Virginia 1990; Mack and Pyke 1984; Pyke 1990).

Harper (1977) suggested that optimal seed bank strategies depended upon the probability of successful reproduction and the rate of seed mortality. If the probability of a seed producing a seed-bearing plant is high, the optimal strategy is for a large proportion of the stored seeds to germinate annually; other losses from the seed bank are unimportant. In this case, the volume of the seed bank fluctuates considerably through the year. This is the strategy adopted by cheatgrass, which despite great seed longevity (Hulbert 1955; Hull 1973), shows little carry over from one year to the next in the seed bank (Mack and Pyke 1983; Thill et al. 1984).

Alternatively, if the probability of successful reproduction is low, the optimal strategy is one of low rates of both germination and seed decay (Harper 1977). Given this circumstance, a stable reserve of propagules from which new seedlings may arise
serves to buffer the plant population and insure its persistence. In a third scenario, if there is a high probability of a low rate of successful reproduction, the rate of seed decay is unimportant if most seeds germinate annually. However, if dormant seeds are produced at a low rate, the rate at which seeds are lost to decay becomes very important. If seeds decay more swiftly than dormancy is broken, mortality will exceed recruitment and the population is doomed. The probability of successful reproduction from seed is likely low for Idaho fescue (e.g. Pyke 1990), and which strategy is followed is unknown.

Interference and Competition

In the literature of plant ecology, discussions of plant interactions have become mired in boiling clouds of semantics. Therefore, I will first give definitions of interference and competition as used in this paper. I employ Harper’s (1977:151) definition of interference: "The presence of a plant changes the environment of its neighbours and may alter their growth rate and form. Such changes in the environment, brought about by the proximity of individuals, may be called ‘interference,’ a blanket term which does not define in any way the manner in which the alterations in environment are produced and includes neighbour effects due to the consumption of resources in limited supply, the production of toxins, or changes in conditions such as protection from wind and influences on the behavior of predators."
Grime (1973:311) defined competition as "the tendency of neighboring plants to utilize the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space," and this is the definition I have used. Keddy (1989:2) offered a more operational definition of competition: "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability." For the experimenter, Keddy's (1989) definition narrows competition to the range of plant interactions that arise from multiple plants attempting to sequester the same finite resource (e.g. molecule of water) with failure being detrimental. Successful competitors consume the resource and benefit, unsuccessful competitors suffer.

Interference by one plant with the growth of another may take the form of a direct interaction, as when two neighboring plants are simultaneously exploring the same soil volume and attempting to withdraw the same soil moisture. Alternatively, the interaction may be indirect, as occurs when attempts to take up soil nutrients are temporally separated because of differing phenologies in neighboring plants. The interaction is clearly detrimental to both plants in the former case. However, in the latter case, the first plant to capture a limited resource is not affected by the subsequent attempt of its neighbor; the neighbor with the later phenology does not lessen the availability of a resource to the plant with the earlier phenology. All ecologists would agree that the direct interaction is a clear example of competition, though they might call it simply competition (e.g. Barbour et al. 1987), interference competition (Keddy 1989), or something else still. The indirect interaction would be
accepted by some ecologists as an example of competition (Keddy (1989) calls it exploitation competition) whereas others would vociferously deny any competitive interaction, instead calling it amensalism (e.g. Burkholder 1952 cited in Radosevich and Holt 1984). In this paper, the use of the word competition will mean that one plant has reduced the availability of a limited resource to another plant. Because of the seasonal and unpredictable availability of soil moisture in semiarid rangelands (see chapter 2; Hidy and Kliefirth 1990; West 1988), the uptake of moisture by a plant with an early phenology reduces the availability of this resource to plants with later phenologies. I accept this as a competitive interaction.

Tilman (1987) noted that phenomenological studies of competition, that is, those that show only that competition has occurred and which competitor was the more successful, are of relatively little value. He calls for studies of competition that elucidate the mechanism or process by which competition occurs. If plants compete for a limited resource, a study of that competition should demonstrate that the resource is limited, the processes (physiological, morphological, phenological) by which competitors acquire the limited resource, and how differences in the strategies of the competitors translate to relative success.

In semiarid rangelands, plants compete for limited soil moisture (Harris 1967; Eissenstat and Caldwell 1988; Melgoza et al. 1990; Smith and Nowak 1990) and minerals (Wilson 1989; Jackson and Caldwell 1989; Eissenstat and Caldwell 1989), such as nitrogen and phosphorus. This competition is manifest by the occupation of space — the volume of soil exploited by a plant’s roots. Generally, the greater the
volume of soil a plant's roots occupy, the more accessible are nutrients and soil moisture (Cornforth 1968; Robinson and Rorison 1985; Caldwell and Richards 1986) though water and nutrient uptake is actually a function of the amount of absorptive surface area (Fitter and Hay 1987; Larcher 1991). In semi-arid grasslands, up to 80% of plant biomass is below ground (Fogel 1985; Caldwell and Richards 1986; Fitter and Hay 1987). The perennial species of Intermountain rangelands are usually deep rooting (Reynolds and Fraley 1989).

In species of semi-arid and arid environments, fitness is increased by attributes which increase water uptake or water use efficiency. Natural selection acts upon the entirety of an organism, and it is the fitness of the organism which determines its persistence and reproductive success. Commonly, allocation to roots is high among species of these habitats, and allocation to roots increases with a decreasing availability of soil resources (Larcher 1991; Fitter and Hay 1987). Root weight ratios increase as the availability of soil water and nutrients decrease and as soil temperature declines. Root weight ratios are higher and less variable in species of stressful environments, where environmental parameters limit the rate at which biomass is accumulated. Typically, species of infertile or shallow soils have low growth rates and high allocation to roots. Species of fertile soils tend to have high growth rates and low root weight ratios. Fitter and Hay (1987:100) suggest the “Root weight ratio is...a good guide to the stressfulness of the environment, but bears little relation to nutrient [and water] absorption.”
A better measure of the capacity of a plant to extract water and nutrients from a soil is root length density (Fitter and Hay 1987). An increase in root density will mean greater exploration and exploitation of a soil volume. The proportion of soil space in the depletion zones surrounding roots will increase with increased root density, and the uptake of immobile nutrients, such as phosphorus and ammonium, will be enhanced. The uptake of mobile nutrients, such as nitrate, and water will also be increased, but not as greatly as that of the immobile nutrients. A greater root density will mean a greater density of root tips. The root hairs associated with root tips have a much smaller diameter, and are able to explore soil micropores too small for roots. Additionally, these root hairs maintain a “liquid junction” for water and nutrient uptake in relatively dry soils, without which contact between root and soil solution would be broken and uptake prevented (Fitter and Hay 1987).

The uptake of soil solution is a passive process, with moisture flowing along the gradient between soil, plant, and atmosphere. Uptake of soil moisture is driven by evapotranspiration from leaves, which gives a water potential gradient between soil and atmosphere. Thus, competition for soil moisture is a function of both transpiring shoot surface area and absorbing root surface area.

Root phenology and morphology are important factors affecting competition among rangeland plants (Harris 1967; Jackson and Caldwell 1989; Eissenstat and Caldwell 1988, 1989; Caldwell and Richards 1986), particularly among seedlings (Harris 1977; Harris and Goebel 1976). In the rangelands of the Pacific Northwest, where precipitation is delivered primarily during the winter, root growth at low soil
temperatures, and thus occupancy of soil volume by spring, may be the deciding factor in competitive interactions among rangeland plants (Harris and Wilson 1970). Additionally, the efficiency of plant species in converting acquired resources to biomass likely influences the outcome of competitive interactions (Svejcar 1990).

Jackson and Caldwell (1989) showed the rate of root growth into fertile microsites within the soil profile to be correlated with the competitive ability of plants. The relative growth rate of ‘Nordan’ crested wheatgrass roots into fertilized microsites was four times greater than the rate for sites receiving only distilled water, and the increase was seen within 24 hours of enrichment. Bluebunch wheatgrass showed no tendency to proliferate roots into fertilized microsites over a two week period.

Similarly, Eissenstat and Caldwell (1989) investigated the dynamics of root growth into disturbed, unoccupied soil patches created by removing neighboring bunchgrasses. Root proliferation by ‘Nordan’ crested wheatgrass was more extensive and more rapid than was that of bluebunch wheatgrass. By transplanting sagebrush seedlings into "dense interspersed stands" of bluebunch wheatgrass and ‘Nordan’ crested wheatgrass, Eissenstat and Caldwell (1988) appraised the relative competitiveness of the two grasses. Sagebrush planted in ‘Nordan’ crested wheatgrass stands had lower survival, growth, reproduction, and late-season water potential than did transplants in bluebunch wheatgrass stands.

Harris (1967) found cheatgrass to attain a significant competitive advantage over bluebunch wheatgrass when the two species germinated in the fall, because of
cheatgrass's root phenology and morphology. In glass tubes containing one seedling each, cheatgrass demonstrated an ability to produce roots at low soil temperatures and occupy a soil during winter, while bluebunch wheatgrass was largely quiescent. Additionally, cheatgrass produced roots which showed a strong positive geotropic response. Bluebunch wheatgrass, on the other hand, produced roots showing a tendency for diageotropic growth. Cheatgrass roots branched little above a depth of 18 to 20 cm, whereas bluebunch wheatgrass roots branched within the upper strata of the soil column.

When bluebunch wheatgrass and cheatgrass were grown in mixture, the roots of the native were relatively ineffective in occupying the soil profile during the first 6 to 8 months following germination (Harris 1967). As a result, cheatgrass was able to exploit a greater portion of stored moisture than was bluebunch wheatgrass during spring and early summer growth. Cheatgrass roots were found in soil which held moisture at a tension no greater than 0.1 MPa throughout its growth period. In contrast, the shallower roots of bluebunch wheatgrass were limited to soil which held moisture at tensions greater than 1.5 MPa during its most active growth. Bluebunch wheatgrass seedlings generally did not survive through the summer as a result of cheatgrass depleting available soil moisture.

Root growth by the native grass was even slower when grown in mixture with cheatgrass than in the competition-free tube, whereas the roots of the alien elongated more rapidly (Harris and Goebel 1976). In a comparison of four grasses currently found on western rangelands, those which had rapidly elongating roots were the most
successful competitors, with water-use efficiency also being an important factor (Harris and Wilson 1970). Bluebunch wheatgrass was the least successful competitor of the four species; the other three, all aliens, were considerably more successful in capturing soil moisture. In a field study, the presence of cheatgrass reduced water potentials in green rabbitbrush and needle-and-thread (*Stipa comata* Trin. & Rupr.), compared to water potentials in the same species not subject to interference from cheatgrass (Melgoza et al. 1990).

Because precipitation is delivered to central Oregon primarily in the winter, spring growth is largely dependent upon stored moisture. In sagebrush-grass communities of south-central Washington, soil moisture accumulated during the October to February period and, despite spring and summer storms, declined throughout the remainder of the year (Cline et al. 1977). Melting snowpacks contribute the majority of soil moisture used by rangeland plants to sustain growth; intense but brief summer thunder storms result in little infiltration (West 1988). The extent and timing of root system development determine, to a large degree, the ability of a rangeland plant to exploit soil moisture. The rooting habit and phenology of cheatgrass imparts a clear competitive advantage in these systems (Harris 1977).

Cheatgrass seedlings generally out-compete seedlings of perennial grasses even when soil temperatures are not limiting (Harris and Goebel 1976; Svejcar 1990). Svejcar (1990) found cheatgrass roots not only elongated more rapidly than did those of crested wheatgrass, but also had greater root length per unit of root biomass. Cheatgrass also accumulated leaf area more rapidly than did crested wheatgrass, and
had greater specific leaf area. The author concluded that the competitive advantage of cheatgrass was due, in part, to the efficiency (per unit biomass) with which the alien converted resources to root length and leaf area. Thus, the ability to germinate and produce roots at low soil temperatures plus conversion efficiency contribute to the advantage enjoyed by cheatgrass in the competitive rangeland environment.

Because Idaho fescue roots are finer than those of cheatgrass (pers. obs.), root length per unit root mass may be comparable to that of cheatgrass; the efficiency with which cheatgrass and Idaho fescue produce roots may be similar. However, bluebunch wheatgrass is more drought tolerant than Idaho fescue (Daubenmire 1970; Tisdale and Hironaka 1981). If the growth rates of bluebunch wheatgrass and Idaho fescue are similar (they evolved in the same system), cheatgrass will likely enjoy a comparable or even greater advantage when competing with Idaho fescue. Rapid growth in cheatgrass would result in greater root length despite an equivalent efficiency per unit biomass in Idaho fescue.

**Literature Cited**


CHAPTER IV. GERMINATION OF IDAHO FESCUE AND CHEATGRASS SEED
UNDER CONDITIONS SIMULATING A CENTRAL OREGON AUTUMN

Jay R. Goodwin, Paul S. Doescher, and Lee E. Eddleman
Introduction

Despite 125 years of abusive grazing and the introduction of cheatgrass 100 years ago, populations of Idaho fescue are still present on degraded central Oregon rangelands. Idaho fescue is a highly palatable native bunchgrass, is selected by both wild and domestic ungulates (Vavra and Sneva 1978; Holechek et al. 1982; Dragt and Havstad 1987), and the abundance of Idaho fescue declines with increasing grazing pressure (Driscoll 1964; Roche 1983; Stubbendieck et al. 1992). The continued presence of Idaho fescue on these degraded rangelands suggests that surviving populations are either less palatable or more competitive ecotypes relative to the original populations. In either case, these persisting populations may offer the potential of restoring Idaho fescue to sites from which it had been eliminated. Neither heavy grazing nor alien invasion has driven these populations into extinction.

If greater competitive abilities were contributing to the persistence of Idaho fescue, then seedlings from these populations should show a greater capacity to compete with cheatgrass seedlings. Cheatgrass seeds germinate in the fall, once sufficient moisture for imbibition is available (Mack and Pyke 1983; Harris 1967). Because early emergence strongly influences the outcome of competitive interactions among seedlings (Ross and Harper 1972; Weiner 1985; Romo and Eddleman 1987), I anticipated that Idaho fescue seed from the disturbed sites would germinate more rapidly and more completely than seed collected from an ungrazed, relict population of Idaho fescue under temperatures characteristic of autumn. Additionally, I wanted
to investigate the influence of moisture stress on germination of seed from the disturbed and undisturbed sites. I predicted that seed of the disturbed-site Idaho fescue populations would show faster germination at elevated water stress than seed from the undisturbed population. Our experiments attempted to achieve the greatest possible biological significance within the constraints of the laboratory; we sought results that would have meaning in the field.

Materials and Methods

**Materials** Seeds of Idaho fescue and cheatgrass were hand-stripped in July, 1989, shortly before seed shatter, at five sites in central Oregon. The different seed accessions are distinguished on the basis of the location of collection (tables 4.1 and 4.2). All accessions, except the Island collection, have very likely been subject to grazing by domestic livestock for the last 125 years, given the history of settlement in central Oregon (e.g. Strong 1940; Galbraith and Anderson 1971; Shinn 1977). The diets of cattle, sheep, and horses are dominated by grasses, and Idaho fescue is a preferred species (Vavra and Sneva 1978). Idaho fescue is a principal grass in the diet of deer (Vavra and Sneva 1978), and elk also prefer Idaho fescue to other forages (Dragt and Havstad 1987). Grazing by domestic livestock on the Island has been very limited because of difficult access and a lack of water. As far as is known, the Island has been grazed only twice by domestic livestock: sheep were driven up onto the Island for two successive summers during the 1920's (Driscoll 1964). The Island
Table 4.1 Collections of Idaho fescue seed used in this research.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Year Collected</th>
<th>Mean Mass(^1)</th>
<th>Grams per 1000 Seeds</th>
<th>Percent Fill(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>1989</td>
<td>0.060a</td>
<td>1.20</td>
<td>54.3</td>
</tr>
<tr>
<td>McCoin Orchard</td>
<td>1989</td>
<td>0.057a</td>
<td>1.14</td>
<td>52.4</td>
</tr>
<tr>
<td>McCoin Orchard</td>
<td>1990</td>
<td>0.038</td>
<td>0.76</td>
<td>19.8</td>
</tr>
<tr>
<td>Blanchard Well</td>
<td>1989</td>
<td>0.057a</td>
<td>1.14</td>
<td>66.8</td>
</tr>
<tr>
<td>Blanchard Well</td>
<td>1990</td>
<td>0.033</td>
<td>0.66</td>
<td>---</td>
</tr>
<tr>
<td>Lone Pine</td>
<td>1989</td>
<td>0.047a</td>
<td>0.94</td>
<td>57.7</td>
</tr>
<tr>
<td>Combs Flat</td>
<td>1989</td>
<td>0.050a</td>
<td>1.00</td>
<td>50.1</td>
</tr>
</tbody>
</table>

1. Mean mass (g) of 50 seeds based on three samples, except for the McCoin collections for which n=6. For all means except McCoin collections SE=0.0041; SE=0.0029 in the McCoin collections.
2. Percent fill = [(cleaned mass ÷ precleaned mass)\(^100\).

Table 4.2 Collections of cheatgrass seed used in the germination experiment.

<table>
<thead>
<tr>
<th>Collection</th>
<th>Year Collected</th>
<th>Mean Mass(^1)</th>
<th>Grams per 1000 Seeds</th>
<th>Percent Fill(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>McCoin Orchard</td>
<td>1989</td>
<td>0.123a</td>
<td>2.47</td>
<td>59.2</td>
</tr>
<tr>
<td>Blanchard Well</td>
<td>1989</td>
<td>0.127a</td>
<td>2.53</td>
<td>68.6</td>
</tr>
<tr>
<td>Lone Pine</td>
<td>1989</td>
<td>0.130a</td>
<td>2.60</td>
<td>65.6</td>
</tr>
<tr>
<td>Combs Flat</td>
<td>1989</td>
<td>0.127a</td>
<td>2.53</td>
<td>65.6</td>
</tr>
</tbody>
</table>

1. Mean mass (g) of 50 seeds based on three samples. For all means SE=0.0041. 2. Percent fill = [(cleaned mass ÷ precleaned mass)\(^100\).

collection of Idaho fescue is taken as representative of an undisturbed population, whereas the remaining collections represent populations that have been disturbed by livestock grazing and invasion by alien annuals.

Collected seeds were mechanically threshed and a seed blower was used to sort filled seeds from chaff and unfilled seeds. Once selected, the blower setting was held
constant for all seed lots within a species. Mean seed mass within the five 1989 Idaho fescue collections or the four cheatgrass collections did not differ following cleaning (Idaho fescue: F = 1.84, p = 0.1811, table 4.1; cheatgrass: F = 0.44, p = 0.7278, table 4.2). Seeds collected in July, 1989 were processed in September of the same year, and were stored at room temperature in paper bags following processing. The experiments were run in 1991 using two year old seed.

In July of 1990, Idaho fescue seed was again collected from the Blanchard Well and McCoin Orchard sites. Seed at the other sites was not available in sufficient quantity; Idaho fescue at the Island site set no seed in 1990. Mean seed mass in 1990, a drought year, was significantly lower for both accessions than in 1989 (Blanchard: t = 4.94, p = 0.004; McCoin: t = 5.16, p = 0.000).

The Results of a Pretest: Water Stress and Germination  Idaho fescue seed can germinate at low temperatures and under moisture stress (Doescher et al. 1985), and the availability of moisture may be the primary factor controlling germination of Idaho fescue. Young and Evans (1982:1) state, "Moisture stress is the major factor limiting establishment of seedlings of desirable perennial forage grasses on sagebrush (Artemisia) rangelands."

A pretest was run to investigate germination of Idaho fescue seed collected from a disturbed site in response to increasing moisture stress. Seeds were germinated in a lighted germinator at a constant temperature of 15 °C on a quilted cellulose substrate (Kimpak®) moistened with distilled water or solutions having
different osmotic potentials. Polyethylene glycol 8000 was used to adjust the potentials of the solutions to -0.2, -0.4, -0.6, and -0.8 MPa (Michel and Kaufmann 1973; Michel 1983). Median response time (the time required for 50% of the seeds that ultimately germinated to have actually done so) increased as the potential of the solution decreased, giving three statistically distinct groups (F=13.67, p<0.05; table 4.1).

<table>
<thead>
<tr>
<th>Treatment (MPa)</th>
<th>0</th>
<th>-0.2</th>
<th>-0.4</th>
<th>-0.6</th>
<th>-0.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Response Time (Days)</td>
<td>9.93a</td>
<td>13.07b</td>
<td>13.58b</td>
<td>13.70b</td>
<td>18.40c</td>
</tr>
</tbody>
</table>

1. Different letters indicate different means at a significance level of 0.05, Bonferroni multiple comparison procedure.

**Methods**  Three completely randomized experiments investigated germination of Idaho fescue seeds. Each experiment simulated a regime of temperature and photoperiod typical of late summer or autumn in central Oregon, and was run in a Hoffman SG-30 Germinator (Hoffman Manufacturing Co.). Conditions typical of August were simulated in one experiment, September in another, and October in the third. The August and September experiments were run concurrently in separate germinators. With the completion of the August simulation, the germinator was reprogrammed to simulate October conditions. Within each experiment, three levels of water potential (0, -0.5, and -1 MPa) simulated wet, intermediate, and dry months.
Seeds were germinated on moistened Kimpak® (Seedburo Equipment Co.) in transparent acrylic germination boxes (11 x 11 x 3 cm; Hoffman Manufacturing Co.). Seeds were evenly distributed over the substrate so that all seeds were in contact with the moistened medium rather than resting upon one another. Thirty-six lots of 50 seeds were counted from each of the five populations using an electronic seed counter (Seedburo Equipment Co.), giving a total of 180 lots (three experiments, five populations, three levels of water potential, four replicates per treatment). In each experiment, 12 lots of seed from each population were randomly assigned to individual germination boxes labeled with water potential, population, and replication number. In all three experiments, fifty seeds in a germination box constituted an experimental unit. Replicates were randomly assigned to one of ten shelves in a germinator with only one replicate of any particular treatment per shelf. Germination boxes were sealed in transparent Ziplock® bags to maintain high humidity.

The programs used to simulate August, September and October temperature and photoperiod regimes in central Oregon were:

**August**  
-- Temperature Regime: 8 °C (6 hrs)/29 °C (18 hrs)  
-- Light Regime: 14 hrs light/10 hrs dark

**September**  
-- Temperature Regime: 4 °C (7 hrs)/23 °C (17 hrs)  
-- Light Regime: 12.5 hrs light/11.5 hrs dark

**October**  
-- Temperature Regime: 1 °C (8 hrs)/ 18 °C (16 hrs)  
-- Light Regime: 11 hrs light/ 13 hrs dark.
A forty year record of climate data (1950 to 1989) was used to determine monthly mean temperatures (Anon. 1983, 1981-1989). The temperatures selected are the mean maximum and minimum for the months of interest, and the duration of each period is based on climatological data from stations surrounding the seed collection sites. Extreme temperatures were selected because temperature fluctuations at the soil surface are greater than those measured in the available macroclimate data, and I lacked soil surface temperature data. Photoperiod was taken as mid-month day length for August, September, and October in the study area (44° 21' N, 120° 54' W). These regimes approximate field conditions (fig. 4.1), though the rate of change between warm and cold periods is more abrupt in the germinator. Lights were on during the warm period, but the warm period always exceeded the lighted period; that is, seeds were exposed to cold and dark, warm and dark, and warm and lighted conditions. Mean photosynthetic photon flux density in the germinator was 32.5 μE m⁻²s⁻¹.

Seeds were germinated under the above environmental conditions in either distilled water (osmotic potential of 0 MPa) or polyethylene glycol 8000 (PEG) (J.T. Baker, Inc.) solutions having osmotic potentials of -0.5 and -1.0 MPa (Michel and Kaufmann 1973; Michel 1983). The amount of PEG required for the solutions was calculated using Michel's (1983) Equation 1. Because the potential of a PEG solution is influenced by temperature, the solutions were prepared to give the desired osmotic potential during the warm period of the alternating temperature regimes. Fungicides were not employed, as they can inhibit germination and because the reaction between
Figure 4.1 Comparison of field and germinator temperatures for a) September and b) October. Continuous temperature data is not available for the August simulation.
PEG and other solutes is synergistic (Michel 1983). The addition of fungicide would have altered the osmotic potential of the solution to an unknown value. Also, healthy seeds are generally resistant to fungal attack (Young and Young 1986). Because a germination substrate can alter the potential of a PEG solution by taking up water but not the larger PEG molecules, effectively increasing the concentration of PEG in solution, the ratio of solution (ml) to substrate mass (g) should be 12 or greater to prevent changes in the potential of the solution (Hardegree and Emmerich 1990). The mean mass of the Kimpak substrate used was 3.49 g (s=0.125); the substrate was moistened with 50 ml of water or PEG solution. The ratio of solution volume to substrate mass was 14.3.

Each germination trial was run for 30 days, and boxes were examined for germinated seeds daily. Germination was defined as emergence of a seminal root or coleoptile of 5 mm length and germinated seeds were removed. After germination commenced, it was considered to have ceased after seven consecutive days with no additional seeds germinating. Ungerminated seeds were not removed from the boxes until an experiment was terminated.

The hypotheses tested were that Idaho fescue seeds collected from disturbed sites would germinate at a greater rate and to a higher percentage under fall temperature and moisture conditions than seed from a relict area (the Island), and that germination would be more strongly inhibited in the Island seed compared to disturbed-site seed under conditions of increasing moisture stress. The null hypotheses were that there would be no differences. The objectives of the experiment
were to determine the days to the start of germination, median response time (time to 50% of the final germination percentage), Maguire’s (1962) coefficient of the rate of germination (CRG), and percent germination for Idaho fescue seeds collected from disturbed (grazed and invaded) and undisturbed sites under conditions representative of fall in central Oregon. To allow comparison, cheatgrass seeds from the four disturbed sites were also germinated and the same variables measured. Separate experiments were run for each species.

Germination percentage equalled the number of germinated seeds divided by the actual number of seeds in the particular replicate, expressed as a percentage. Days to germination equaled the number of days that passed before the first seed germinated. Median response times were calculated from the number of seeds that actually germinated in each replicate. The time required for 50% of these seeds to germinate equaled the median response time.

The CRG values were calculated as:

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

where \( N_i \) is the number of seeds germinating on the \( i^{th} \) day and \( T_i \) is the \( i^{th} \) day from sowing. The CRG is very sensitive to early responses, as a seed germinating on the first day following sowing carries 30 times the weight of a seed germinating on the 30th day of a trial. Thus, a high CRG reflects rapid and probably extensive germination whereas a low CRG reflects slower germination, and probably a less complete response. Germination coefficients such as the CRG have been criticized
for confounding the effects of time of response and number of seeds responding (Scott et al. 1984; Brown and Mayer 1986). However, because early emergence confers substantial advantages to seedlings in a competitive environment (Ross and Harper 1972; Weiner 1985), the CRG retains interpretable ecological significance at the level of the population.

Statistical analyses of the experiments were made using Number Cruncher Statistical System™ (Hintze 1990). For each population within an experiment, results were tested and plotted to determine normality and equality of variance. Normality was tested using D’Agostino’s univariate normality tests ($\alpha = 0.01$), which include skewness and kurtosis tests and an omnibus normality test, along with normal probability plots using 95% confidence limits. The $T^2$ multivariate outlier test ($\alpha =0.01$) was used to test for outliers. The Bartlett-Box homogeneity test was used to test for equal variances ($\alpha =0.01$).

The response variables (percent germination, days to germination, median response time, and CRG) passed the normality, outlier, and homogeneity of variance tests. Therefore, untransformed data were analyzed using two-factor ANOVA with contrasts of totals to test the hypothesized differences between the disturbed and undisturbed populations. The two factors in the ANOVA were population (Combs Flat, Lone Pine, Blanchard, McCoin, and Island) and water potential (0, -0.5, and -1.0 MPa) and a separate ANOVA was run for each response variable. Given a significant F-test ($\alpha =0.05$), Fisher’s Protected LSD was used to separate means at a significance level of 0.05 to identify differences among the five populations.
The cheatgrass germination trial was identical in design, methodology, and analysis to the Idaho fescue trial, though four rather than five seed populations were tested. The cheatgrass trial was run concurrently with the Idaho fescue trial, so that germination of both species under a particular light and temperature regime was tested at the same time in the same germinator. Analysis of the cheatgrass results required that two variables, days to germination and CRG, be transformed, using the natural logarithm, to satisfy assumptions of equal variance and normality. To allow comparison with the untransformed Idaho fescue results, untransformed means are reported for these variables, with differences among means determined using the transformed data.

Results

**Idaho fescue**  More Idaho fescue seeds from the undisturbed population germinated in all three experiments compared to the populations from disturbed sites (table 4.4). Within the two Idaho fescue groups, percent germination was the same in the September and October experiments. Fewer seeds germinated under August conditions for both groups. In the August and September experiments, percent germination did not change as water potential changed from 0.0 to -0.5 MPa (table 4.5). Lowering water potential further to -1.0 MPa resulted in significantly fewer seeds germinating in both experiments, however. Under the cooler conditions of the
Table 4.4  Germination responses under simulated autumn conditions of Idaho fescue seed collected from populations on disturbed and undisturbed sites.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Undisturbed&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Disturbed&lt;sup&gt;2&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>August</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>74.95a</td>
<td>2.134</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>7.17a</td>
<td>0.400</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>12.50a</td>
<td>0.453</td>
</tr>
<tr>
<td>CRG</td>
<td>3.42a</td>
<td>0.105</td>
</tr>
<tr>
<td>September</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>87.84a</td>
<td>1.767</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>5.75a</td>
<td>0.313</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>10.17a</td>
<td>0.397</td>
</tr>
<tr>
<td>CRG</td>
<td>5.02a</td>
<td>0.110</td>
</tr>
<tr>
<td>October</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>86.30a</td>
<td>1.635</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>8.83a</td>
<td>0.258</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>14.08a</td>
<td>0.293</td>
</tr>
<tr>
<td>CRG</td>
<td>3.71a</td>
<td>0.083</td>
</tr>
</tbody>
</table>

Within a row, different letters indicate significant differences (α=0.05). 1. n=12  2. n=48

October experiment, percent germination decreased with increasing water stress. In both the August and October experiments, percent germination was influenced by both water potential (August: F=82.76, p<0.000; October: F=35.68, p<0.000) and population (August: F=3.52, p=0.014; October: F=4.03, p=0.007). In the September experiment, only water potential (F=35.31, p<0.000) significantly
Table 4.5 Effect of water stress on germination responses of Idaho fescue seed under simulated autumn conditions.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Water Potential (MPa)</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.0</td>
<td>-0.5</td>
</tr>
<tr>
<td><strong>August</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>77.04a</td>
<td>77.45a</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>4.65a</td>
<td>7.10b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>7.85a</td>
<td>13.90b</td>
</tr>
<tr>
<td>CRG</td>
<td>4.53a</td>
<td>2.88b</td>
</tr>
<tr>
<td><strong>September</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>89.83a</td>
<td>88.39a</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>3.95a</td>
<td>5.70b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>6.35a</td>
<td>11.25b</td>
</tr>
<tr>
<td>CRG</td>
<td>6.77a</td>
<td>4.09b</td>
</tr>
<tr>
<td><strong>October</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>89.57a</td>
<td>84.70b</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>5.45a</td>
<td>8.30b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>8.25a</td>
<td>13.95b</td>
</tr>
<tr>
<td>CRG</td>
<td>5.17a</td>
<td>3.04b</td>
</tr>
</tbody>
</table>

Within a row, different letters indicate significant differences (α=0.05). 1. n = 20 for all means.

affected the extent of germination. (The p-value for population in the September experiment was 0.051.)

Seeds from the undisturbed Idaho fescue population began germinating earlier than seed from the disturbed-site populations in the August experiment (table 4.4). In contrast, there were no differences between the two Idaho fescue groups in days to germination under September and October conditions. For both groups, seed began
germinating most quickly in the September experiment. More time passed before seeds began germinating under October conditions than in either of the two warmer experiments. Increasing water stress resulted in longer delays before seeds began germinating (table 4.5). Germination occurred earliest at 0.0 MPa and latest at -1.0 MPa in all three experiments. Days to germination were fewest under September conditions at all levels of water potential. Seeds began germinating about a day earlier under August conditions compared to October conditions at each level of water stress. In the August and September experiments, days to germination varied with water potential (August: F=170.14, p<0.000; September: F=121.92, p<0.000), but water potential (F=444.65, p<0.000) and population (F=3.49, p=0.015) had significant influences in the October experiment.

Idaho fescue seeds from the undisturbed site not only began germinating sooner than seeds from the disturbed-site populations, they also germinated at a greater rate. Median response times were consistently shorter for the undisturbed seed than for seed from the disturbed sites in all experiments (table 4.4). The median response was attained most quickly by both Idaho fescue groups in the September experiment, and most slowly under October conditions. Increasing water stress always increased the median response time (table 4.5). In all three experiments, reducing water potential water potential from 0.0 to -0.5 MPa roughly doubled median response times. At -1.0 MPa, median response times were almost three times longer than at 0.0 MPa. The rate of seed germination was greatest in the September experiment at each level of water stress, and lowest under October conditions.
Median response times varied with both water potential (August: \( F=316.83, \) \( p<0.000 \); September: \( F=246.52, \) \( p<0.000 \); October: \( F=950.08, \) \( p<0.000 \)) and population (August: \( F=5.65, \) \( p<0.001 \); September: \( F=3.98, \) \( p<0.008 \); October: \( F=3.15, \) \( p<0.023 \)) in the three experiments.

Showing the same trends as percent germination, days to germination, and median response times, CRG's of Idaho fescue seed from the undisturbed site were higher than those of seed from the disturbed sites in all three experiments (table 4.4). For both groups, CRG's were highest under September conditions and lowest under August conditions. Increasing water stress always sharply reduced the CRG (table 4.5). Reducing water potential from 0.0 to -0.5 MPa roughly halved CRG values, and CRG's were again halved when water potential was dropped to -1.0 MPa. In the September experiment, both water potential (\( F=688.15, \) \( p<0.000 \)) and population (\( F=11.86, \) \( p<0.000 \)) were significant factors affecting CRG. In the August (table 4.6) and October (table 4.7) experiments, the interactions of water potential and population were significant (August: \( F=3.02, \) \( p=0.008 \); October: \( F=2.93, \) \( p=0.010 \)).

On the level of the individual populations, more seeds from the undisturbed Island population germinated under August conditions than in any of the four populations from disturbed sites (fig. 4.2). Within the disturbed-site populations, Combs Flat seeds gave the greatest response. Fewer seeds from the Lone Pine, Blanchard, and McCoin populations germinated. Under the cooler conditions of the September and October experiments, one or more of the disturbed-site populations
Table 4.6 Two-way interaction means for CRG of Idaho fescue seed under August temperature and photoperiod conditions.

<table>
<thead>
<tr>
<th>$\Psi$ (MPa)</th>
<th>Population</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Combs Flat</td>
<td>Lone Pine</td>
</tr>
<tr>
<td>0.0</td>
<td>4.7509</td>
<td>4.8030</td>
</tr>
<tr>
<td>-0.5</td>
<td>2.4627</td>
<td>2.7576</td>
</tr>
<tr>
<td>-1.0</td>
<td>1.3586</td>
<td>1.0541</td>
</tr>
<tr>
<td>Mean</td>
<td>2.8574 a</td>
<td>2.8716 a</td>
</tr>
</tbody>
</table>

Standard errors: two-way interaction means = 0.1446; population means = 0.0835; water potential means = 0.0647.

Table 4.7 Two-way interaction means for CRG of Idaho fescue seed under the October regime of temperature and photoperiod.

<table>
<thead>
<tr>
<th>$\Psi$ (MPa)</th>
<th>Population</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Combs Flat</td>
<td>Lone Pine</td>
</tr>
<tr>
<td>0.0</td>
<td>4.3748</td>
<td>5.4287</td>
</tr>
<tr>
<td>-0.5</td>
<td>2.3080</td>
<td>3.2721</td>
</tr>
<tr>
<td>-1.0</td>
<td>1.5689</td>
<td>1.6802</td>
</tr>
<tr>
<td>Mean</td>
<td>2.7506 a</td>
<td>3.4604 b</td>
</tr>
</tbody>
</table>

Standard errors: two-way interaction means = 0.1446; population means = 0.0835; water potential means = 0.0647.

had the same percent germination as the Island population. Combs Flat seeds had the poorest germination in both the September and October experiments. For all five Idaho fescue populations, more seeds germinated under the cooler conditions of September and October than in the warmer August experiment.
Figure 4.2 Germination of seed from five Idaho fescue populations under conditions simulating autumn in central Oregon.
Island seeds also began germinating earlier than any seeds from the disturbed-site populations in the August experiment (fig. 4.3). Seeds of the Combs Flat and Lone Pine populations were the slowest to begin germinating. In the September experiment, Blanchard seeds began germinating as quickly as Island seeds. Seeds from the McCoin population were the slowest to begin germinating under September conditions. McCoin seeds were also the slowest to germinate in the October experiment. Island, Blanchard, and Combs Flat began germinating the earliest under October conditions. For all populations, seeds began germinating most quickly in the September experiment, slower under the warmer conditions of the August experiment, and most slowly in the cool October experiment.

The rate of germination was greatest in Island seeds in all three experiments, and McCoin seeds had the lowest rate (fig. 4.4). Combs Flat, Lone Pine, and Blanchard consistently had intermediate germination rates. Germination was most rapid in the September experiment for all five populations. The cool conditions of the October experiment allowed the slowest rates of germination, with warm August conditions producing an intermediate rate of germination.

Island seeds consistently had the highest CRG's of the five populations in the three experiments (fig. 4.5). Combs Flat seeds tended to have the lowest CRG's. The Lone Pine, Blanchard, and McCoin populations had equivalent CRG's in each of the three experiments. Across all populations, CRG values were highest in the September experiment and lowest under August conditions.
Figure 4.3 Days to initial germination of seed from five Idaho fescue populations germinated under conditions simulating autumn in central Oregon.
Figure 4.4 Median response times of seed from five Idaho fescue populations germinated under conditions simulating autumn in central Oregon.
Figure 4.5 CRG's of seed from five Idaho fescue populations germinated under conditions simulating autumn in central Oregon.
Cheatgrass. The four cheatgrass populations differed in seed viability, but the different temperatures of the three experiments had no effect on percent germination (table 4.8). Seeds from the McCoin population achieved about 91% germination in the three experiments, and Blanchard seed about 82%. Germination was considerably poorer in the Lone Pine and Combs Flat seeds, with roughly 57 and 44% germination, respectively, across the three experiments. In general, the extent of cheatgrass seed germination was largely insensitive to water stress (table 4.9). Only when water potential was reduced to -1.0 MPa under September conditions did fewer seeds germinate compared to water potentials of 0.0 and -0.5 MPa. Oddly, seed from the Blanchard population achieved better germination with increasing water stress in the October simulation (table 4.10). This is likely due, in part, to the effects of deawning and cleaning the seeds prior to the test. About a third of the seeds that failed to germinate in the 0.0 and -0.5 MPa treatments lacked their lemma and palea (see discussion below).

Population (F=126.38, p<0.000) was the only significant factor affecting percent germination of cheatgrass seed in the August simulation; the interaction of population x water potential just barely failed the significance test (F=2.36, p=0.0501). Both population (F=275.71, p<0.000) and water potential (F=9.09, p<0.000) were significant under September conditions, and the interaction of these two factors (F=3.94, p=0.004) was significant in the October simulation. The
Table 4.8 Responses of cheatgrass seed collected from four populations and germinated under simulated autumn conditions.  

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Population</th>
<th>Combs Flat</th>
<th>Lone Pine</th>
<th>Blanchard</th>
<th>McCoin</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>August</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>47.29c</td>
<td>57.83b</td>
<td>82.55a</td>
<td>88.59a</td>
<td>1.751</td>
<td></td>
</tr>
<tr>
<td>Days to Germination</td>
<td>2.33a</td>
<td>2.08a</td>
<td>2.00a</td>
<td>2.00a</td>
<td>0.224</td>
<td></td>
</tr>
<tr>
<td>Median Response Time</td>
<td>6.17cd</td>
<td>5.92bcd</td>
<td>5.25abc</td>
<td>4.92ab</td>
<td>0.258</td>
<td></td>
</tr>
<tr>
<td>CRG</td>
<td>5.97c</td>
<td>8.06b</td>
<td>13.58a</td>
<td>13.76a</td>
<td>0.459</td>
<td></td>
</tr>
<tr>
<td><strong>September</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>40.67d</td>
<td>57.95c</td>
<td>81.08b</td>
<td>91.16a</td>
<td>1.371</td>
<td></td>
</tr>
<tr>
<td>Days to Germination</td>
<td>1.67a</td>
<td>1.50a</td>
<td>1.58a</td>
<td>1.67a</td>
<td>0.138</td>
<td></td>
</tr>
<tr>
<td>Median Response Time</td>
<td>3.67b</td>
<td>3.17a</td>
<td>3.08a</td>
<td>3.33ab</td>
<td>0.142</td>
<td></td>
</tr>
<tr>
<td>CRG</td>
<td>7.25c</td>
<td>10.59b</td>
<td>16.45a</td>
<td>18.48a</td>
<td>0.610</td>
<td></td>
</tr>
<tr>
<td><strong>October</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>45.37d</td>
<td>56.44c</td>
<td>82.87b</td>
<td>91.77a</td>
<td>1.589</td>
<td></td>
</tr>
<tr>
<td>Days to Germination</td>
<td>3.42a</td>
<td>3.33a</td>
<td>3.33a</td>
<td>3.33a</td>
<td>0.072</td>
<td></td>
</tr>
<tr>
<td>Median Response Time</td>
<td>5.75a</td>
<td>5.42a</td>
<td>4.58a</td>
<td>5.25a</td>
<td>0.357</td>
<td></td>
</tr>
<tr>
<td>CRG</td>
<td>4.51c</td>
<td>5.78b</td>
<td>9.26a</td>
<td>10.75a</td>
<td>0.232</td>
<td></td>
</tr>
</tbody>
</table>

1. n=12 for all means. Within a row, different letters indicate significant differences (α=0.05).  

The explanatory power of population was consistently greater than that of water potential for percent germination across the three simulations, based on mean squares.
Table 4.9 Effect of water stress on germination of cheatgrass seed under simulated autumn conditions.

<table>
<thead>
<tr>
<th>Simulation</th>
<th>Water Potential (MPa)</th>
<th>Standard Error</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.0</td>
<td>-0.5</td>
</tr>
<tr>
<td><strong>August</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>68.08a</td>
<td>70.17a</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>1.00a</td>
<td>1.88b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>2.19a</td>
<td>3.94b</td>
</tr>
<tr>
<td>CRG</td>
<td>16.70a</td>
<td>10.00b</td>
</tr>
<tr>
<td><strong>September</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>70.92a</td>
<td>68.38a</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>1.00a</td>
<td>1.50b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>2.06a</td>
<td>3.13b</td>
</tr>
<tr>
<td>CRG</td>
<td>19.87a</td>
<td>12.61b</td>
</tr>
<tr>
<td><strong>October</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Germination (%)</td>
<td>69.50a</td>
<td>70.28a</td>
</tr>
<tr>
<td>Days to Germination</td>
<td>2.06a</td>
<td>3.06b</td>
</tr>
<tr>
<td>Median Response Time</td>
<td>3.25a</td>
<td>4.75b</td>
</tr>
<tr>
<td>CRG</td>
<td>10.89a</td>
<td>7.50b</td>
</tr>
</tbody>
</table>

Within a row, different letters indicate significant differences (α=0.05). 1. n = 20 for all means.

Days to the start of germination did not differ among the four populations in any of the three simulations (table 4.8), but germination was delayed by increasing water stress (table 4.9). Cheatgrass seed began germinating very quickly at all levels of water stress, with only 1-2 days passing before seeds began germinating when
Table 4.10 Two-way interaction means for percent germination of cheatgrass seed under the October regime of temperature and photoperiod.

<table>
<thead>
<tr>
<th>$\Psi$ (MPa)</th>
<th>Combs Flat</th>
<th>Lone Pine</th>
<th>Blanchard</th>
<th>Mc Coin</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>46.49</td>
<td>57.97</td>
<td>76.96</td>
<td>96.56</td>
<td>69.50a</td>
</tr>
<tr>
<td>-0.5</td>
<td>45.01</td>
<td>57.89</td>
<td>82.73</td>
<td>95.44</td>
<td>70.28a</td>
</tr>
<tr>
<td>-1.0</td>
<td>44.57</td>
<td>53.47</td>
<td>88.93</td>
<td>83.31</td>
<td>67.57a</td>
</tr>
<tr>
<td>Mean</td>
<td>45.37d</td>
<td>56.44c</td>
<td>82.87b</td>
<td>91.77a</td>
<td></td>
</tr>
</tbody>
</table>

Standard errors: two-way interaction means = 2.7526; population means = 1.5892; water potential means = 1.3763.

Water potential was 0.0 MPa and 2-5 days at -1.0 MPa. Germination started earliest under September conditions and latest under October conditions. In all three simulations, water potential proved to be the only significant factor affecting time to the start of germination (August: $F=79.91$, $p<0.000$; September: $F=32.55$, $p<0.000$; October: $F=513.82$, $p<0.000$).

In general, the Mc Coin and Blanchard seed populations germinated the most rapidly and seeds from Combs Flat the slowest. However, all four populations had equivalent median response times in the October experiment, and only the Combs Flat seed was slower than the other populations under September conditions (Table 4.8). Differences in median response times among the four populations were not consistent in the three experiments. The rate of germination was greatest in the September experiment, and slower in both the warmer August and cooler October experiments. Median response times consistently increased with increasing water stress (Table 4.9).
The inhibitory effect of water stress was reduced under conditions simulating September, suggesting a temperature x water potential interaction. In the August and September simulations, median response time varied with both population (August: $F=5.03$, $p=0.005$; September: $F=3.29$, $p=0.032$) and water potential (August: $F=390.99$, $p<0.000$; September: $F=120.60$, $p<0.000$), but only water potential ($F=54.98$, $p<0.000$) proved significant under October conditions.

Differences in CRG's of the four seed populations reflect differences in rates of germination. The McCoin and Blanchard populations had the highest CRG's in all three experiments, and Combs Flat the lowest (table 4.8). The CRG's were highest under conditions simulating September and lowest under October conditions. Increasing water stress always reduced CRG, though CRG's were higher at all levels of water stress under September conditions than in the other two experiments (table 4.9). Water potential ($F=256.92$, $p<0.000$) and population ($F=70.21$, $p<0.000$) were both significant factors affecting CRG in the August simulation; the interaction of these two factors barely failed the significance test ($p=0.051$). In both the September (table 4.11) and October (table 4.12) simulations, the interactions of water potential and population were significant (September: $F=2.43$, $p=0.045$; October: $F=5.47$, $p=0.000$).
Table 4.11 Two-way interaction means for CRG of cheatgrass seed under the September regime of temperature and photoperiod.

<table>
<thead>
<tr>
<th>Ψ (MPa)</th>
<th>Combs Flat</th>
<th>Lone Pine</th>
<th>Blanchard</th>
<th>McCain</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>10.83</td>
<td>14.61</td>
<td>23.58</td>
<td>30.44</td>
<td>19.87a</td>
</tr>
<tr>
<td>-0.5</td>
<td>7.24</td>
<td>10.29</td>
<td>17.41</td>
<td>15.49</td>
<td>12.61b</td>
</tr>
<tr>
<td>-1.0</td>
<td>3.69</td>
<td>6.88</td>
<td>8.35</td>
<td>9.52</td>
<td>7.11c</td>
</tr>
<tr>
<td>Mean</td>
<td>7.25c</td>
<td>10.59b</td>
<td>16.45a</td>
<td>18.48a</td>
<td></td>
</tr>
</tbody>
</table>

Standard errors: two-way interaction means = 1.0572; population means = 0.6104; water potential means = 0.5286.

Table 4.12 Two-way interaction means for CRG of cheatgrass seed under the October regime of temperature and photoperiod.

<table>
<thead>
<tr>
<th>Ψ (MPa)</th>
<th>Combs Flat</th>
<th>Lone Pine</th>
<th>Blanchard</th>
<th>McCain</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>6.35</td>
<td>8.23</td>
<td>12.05</td>
<td>16.91</td>
<td>10.89a</td>
</tr>
<tr>
<td>-0.5</td>
<td>4.62</td>
<td>5.42</td>
<td>9.61</td>
<td>10.34</td>
<td>7.50b</td>
</tr>
<tr>
<td>-1.0</td>
<td>2.56</td>
<td>3.70</td>
<td>6.11</td>
<td>4.99</td>
<td>4.34c</td>
</tr>
<tr>
<td>Mean</td>
<td>4.51c</td>
<td>5.78b</td>
<td>9.26a</td>
<td>10.75a</td>
<td></td>
</tr>
</tbody>
</table>

Standard errors: two-way interaction means = 0.4014; population means = 0.2317; water potential means = 0.2007.

Discussion

This experiment focused on the germination of Idaho fescue seed under conditions that simulated autumn in central Oregon. I tested the hypothesis that Idaho
fescue populations that were persisting on degraded, cheatgrass-invaded rangelands represented more competitive ecotypes compared to Idaho fescue from an undisturbed relict area. Idaho fescue reproduces by seed (Roche 1983; Stubbendieck et al. 1992). I therefore reasoned that for Idaho fescue populations to persist despite competition from cheatgrass for soil resources, Idaho fescue seedlings must successfully compete with cheatgrass seedlings. I predicted that seeds from the invaded sites would show germination responses that were similar to those of cheatgrass seed (i.e. rapid germination, relative insensitivity to cool temperatures and low moisture availability) whereas seeds from the undisturbed site would not. Specifically, I expected higher final germination percentages and faster rates of germination in the seeds from disturbed sites if the hypothesis was true.

The results do not support the hypothesis of increased competitiveness in the germination responses of seed from the disturbed sites. In each of the three simulations, more of the seeds from the undisturbed Island population germinated compared to the disturbed populations. Of even greater ecological significance, the seeds from the disturbed sites were either slower or no faster to start germinating than were the Island seeds. Early emergence is of great importance in a competition among seedlings for occupation of space and resource capture (Ross and Harper 1972; Jordan 1983; Mithen et al. 1984; Romo and Eddleman 1987). Success in the competition for resources allows growth, which leads to the development of size hierarchies, and seedling mortality is concentrated among the smaller size classes
(Weiner 1985). As Ross and Harper (1972:87) noted, "an individual’s potential for capturing resources is dictated by the number and proximity of neighbors already capturing resources." As little as a day’s difference in time of emergence can determine which of two competing seedling survives and which dies. In winter wheat, interference from cheatgrass reduced yield by 20-30% even when cheatgrass emerged a week after the wheat; if wheat emerged two weeks before cheatgrass, yields were not reduced (Wicks 1966 cited in Thill et al. 1984). On Intermountain rangelands, where growth is dependent upon moisture delivered outside the growing season, depletion of soil moisture from the space accessible to the roots of a newly germinated seedling by a neighbor which emerged earlier likely consigns the late-emerging seedling to desiccation and death. Only in the rarest of instances is moisture delivered during the growing season in sufficient quantity and frequency to mitigate competition from neighboring seedlings on Intermountain rangelands.

Median response time was also attained as soon or sooner by seeds from the undisturbed site compared to seeds from disturbed sites in all three simulations. The implications of a more rapid rate of germination, as evidenced by a shorter median response time, parallel those associated with days to germination. However, median response time is a better variable for comparing responses at the level of the population. Any natural population can be expected to show variability, and days to germination expresses variation at the level of the individual. A few seeds capable of rapid germination may not have a substantial influence on the dynamics of a plant
population if the majority of seeds are slow to germinate while those of competitors germinate sooner. On the whole, Island seed achieved a higher rate of germination than did any of the seed from disturbed sites under all conditions. Similarly, Island seeds had much better CRG’s in all three simulated regimes. Both the rate and extent of germination were greater in Island seeds than in seeds from the disturbed sites. In a race against cheatgrass for establishment, seed from the Island will have a better chance of winning than would seed from one of the disturbed sites. However, because cheatgrass seed began germinating after 1.5 to 3.5 days, and germination began in the Island Idaho fescue seed after 5.8 to 9 days, even Island seedlings have little chance of out-competing cheatgrass seedlings. Clearly, persistence of Idaho fescue on cheatgrass-invaded sites is not due to a germination response that more closely resembles that of the invader.

Water stress greatly influenced the rate of seed germination in the disturbed and undisturbed Idaho fescue and cheatgrass seed groups. As water stress increased, days to germination and median response time increased and CRG decreased. Total germination of Idaho fescue seed was reduced at -1.0 MPa in all regimes, but the magnitude of the effect decreased as temperatures decreased. Cheatgrass seed generally attained the same germination percentage regardless of the level of water stress. Osmotic potentials of 0 and -0.5 MPa supported equivalent total germination in Idaho fescue, except under the cool conditions of October when germination declined with water potential. Island seed tended to achieve higher total germination
than Idaho fescue seed from the disturbed sites in all three regimes, regardless of water stress level, but the differences narrowed as temperature was lowered. Island seed consistently had the shortest median response times, but seeds from one or more of the disturbed populations often began germinating as soon as did Island seeds. Though increasing water stress always decreased the rate of germination, germination was faster in Island seed than in Idaho fescue seed from a disturbed population at all levels of water stress and in all three regimes. However, regardless of the population, increasing water stress always significantly reduced CRG. Germination was 2-5 times slower among Idaho fescue seed populations compared to cheatgrass seed.

The poor germination of Lone Pine and Combs Flat cheatgrass seed was surprising, and is probably an artifact of seed processing. All the seeds used in these experiments were collected, threshed, and cleaned in the summer and fall of 1989. The seed lots were two years old when the germination tests were conducted. Almost invariably, the cheatgrass seeds which failed to germinate had lost their lemma and palea in processing. These two structures are important in enforcing dormancy in grass embryo, primarily by limiting gas exchange and thereby inhibiting metabolic activity (Simpson 1990). Grass seeds from which the lemma and palea have been removed have reduced longevity in storage (Benech Arnold et al. 1992; Justice and Bass 1978). The disparity in seed viability remains an interesting question, however, as cheatgrass seed lots were processed in the same manner and there were no
differences in mass among the four cheatgrass seed collections. Of the four sites, Combs Flat and Lone Pine have received the most intense grazing and are in poorer condition than the other sites. The Blanchard seed was collected from a rocky fence row that provides a refuge from grazing livestock. The McCoin site is in the best condition of the four sites. Grazing leads to nutrient redistribution and export from native rangelands, particularly of nitrogen. The greater susceptibility of the Lone Pine and Combs Flat seed to mechanical injury may be a maternal effect caused by nutrient deficiency. Soil chemical analyses show lower nitrogen levels at these two sites than at the other three, particularly of NH₄-N, though Blanchard also is nitrogen poor. Benech Arnold et al. (1992) showed the dormancy-enforcing effects of glumes depended upon the water relations of the maternal plant during seed production. A genetic basis for the susceptibility to injury cannot be ruled out, but is unlikely given the extremely low genetic variation in cheatgrass (1.05 alleles per locus, 4.6% polymorphic loci with 2.05 alleles per locus, no observed heterozygosity) across its entire North American range (Novak et al. 1991).

The patterns seen in the germination of Idaho fescue and cheatgrass seed demonstrate adaptation to the semiarid rangeland environment. The availability of moisture for imbibition is the most influential factor affecting germination of after-ripened Idaho fescue and cheatgrass seed. This is in agreement with Harper’s (1977) statement of the pre-eminent role of moisture in triggering seed germination in environments characterized by the unpredictability of precipitation. The interaction of
temperature with moisture also shows adaptation. Regardless of the level of water stress, germination was inhibited by warm temperatures in the August simulation. If moisture were the sole factor affecting seed germination, the warm conditions of August should have supported very rapid and extensive germination when seeds were not moisture stressed. In fact, more Idaho fescue seeds germinated under the cooler conditions of September and October, at all levels of moisture stress. Germination of Idaho fescue seed was promoted by the temperatures of the September simulation, whereas both the warmer and cooler temperatures of the August and October simulations, respectively, reduced either germination rate or extent. Cheatgrass seeds germinated most rapidly under September conditions as well. Previous work (Doescher 1983; Buman and Abernathy 1988; Young et al. 1981; Thill et al. 1979; Hulbert 1955) suggests optimum temperatures for both Idaho fescue and cheatgrass seed germination are between 20 and 25 °C. Warm temperatures were 29, 23, and 18 °C in the August, September, and October experiments, respectively.

Long-term climate records show August to be the warmest and driest month of the year. Seedlings emerging in August are very likely to die from lack of moisture. Mack and Pyke (1984) found desiccation to be the major cause of death among cheatgrass seedlings emerging in autumn. Seedling survival on Intermountain rangelands during autumn is greatly influenced by the temporal distribution of precipitation. September is a much wetter month, averaging about twice as much precipitation as August, and October is wetter still. November is even wetter than the
preceding months but the mean daily temperature is so low (3.4 °C) that growth by
native perennial bunchgrasses is most likely inhibited. October temperatures are
much more favorable for growth (mean daily temperature = 9.2 °C), but seedlings
emerging in October would soon be subject to the inhibitory temperatures of
November. Emergence in September would allow up to nine weeks of growth before
low temperatures induced quiescence. Germination during September offers the best
compromise between moisture availability and favorable temperatures to be had in late
summer and autumn in central Oregon. Mack and Pyke (1983) suggested the
existence of fairly well-defined periods during which autumn emergence is late
enough to escape desiccation but early enough to allow sufficient growth to survive
any subsequent grazing or winter injury.

Among the Idaho fescue seed, the Island population showed the least
sensitivity to moisture stress and temperature. Seeds from the Island germinated
faster and to a greater extent than the four populations from disturbed sites.
Cheatgrass seed is relatively insensitive to moisture and temperature (Thill et al.
1979; Young and Evans 1982; Harris 1967; Hulbert 1955 and this study). I interpret
the germination of cheatgrass seed as a strategy for winning the competition for
scarce soil moisture: start quickly. The capture of soil resources is a function of the
area of soil explored; greater root length (or morphological plasticity of the root
system) means greater resource capture (Cornforth 1968; Chapin 1980; Crick and
Grime 1987; Jackson and Caldwell 1989). To sustain growth, a plant must have
sufficient water to maintain turgor and sustain cell elongation while losing moisture during CO₂ uptake. Of the Idaho fescue seed populations studied, all were much slower to germinate than cheatgrass, irrespective of the intensity of water stress. Seed from the Island population of Idaho fescue came the closest to cheatgrass in terms of speed and extent of germination. The Island seed showed the most competitive germination response of the five Idaho fescue populations tested.

Literature Cited


CHAPTER V. AFTER-RIPENING IN IDAHO FESCUE SEED

Jay R. Goodwin, Paul S. Doescher, Lee E. Eddleman
Seed germination may be prevented, despite favorable conditions, by seed dormancy (Harper 1977; Simpson 1990). Seed dormancy is an adaptive trait, allowing for dispersal before germination and avoidance of temporary periods of competition from neighboring plants or conditions unsuitable for growth. Dormancy is one element in the strategy for survival in spatially and temporally heterogeneous environments (Fitter and Hay 1987; Simpson 1990). Simpson (1990:19) stated, “seed dormancy in grasses is general rather than exceptional.” Dormancy may be caused by several factors, including embryo immaturity at dispersal, inhibitory compounds in the seedcoat or endocarp, and structural barriers to moisture uptake or gas exchange (Nelson and Wilson 1969; Copeland and McDonald 1985; Simpson 1990; Benech Arnold et al. 1991, 1992).

Most grasses produce seeds that are partially nondormant at the time of seed shatter. Grime et al. (1981) found germinabilty of fresh seed to be greater in Poaceae than in Asteraceae, Fabaceae, Cyperaceae, and Apiaceae. However, germinability of grass seed varies substantially among species and within populations of the same species following seed maturation (Nelson and Wilson 1969; Shaidaee et al. 1969; Harper 1977; Simpson 1990; Benech Arnold et al. 1992). For example, fresh seeds of squirreltail germinated as well as seeds that had after-ripened from three to six months (Young and Evans 1977), whereas seeds of Sandberg’s bluegrass required six months of after-ripening before maximum germination was obtained (Evans et al.
1977). As both these species are natives and are common on Intermountain rangelands, they illustrate differing adaptive strategies to the same suite of environmental pressures.

Exposure to low temperature is required by seeds of many temperate species before germination will occur (Fitter and Hay 1987). In wild oat (*Avena fatua* L.), low temperature shortens, and may break, dormancy of imbibed seeds whereas high temperatures enforce dormancy (Simpson 1990). The effects of temperature on dormancy in dry seeds differ from those in hydrated seeds. Low temperatures enforce dormancy in grass seeds during dry storage; high temperatures have the opposite effect (Simpson 1990). Germinability of grass seed generally increases over the first year or two following seed production as after-ripening occurs and dormancy is broken (Rice 1989; Grime et al. 1981; Evans et al. 1977; Shaidaee et al. 1969). As after-ripening occurs and dormancy weakens, the range of environmental conditions inducing germination broadens (Simpson 1990).

Idaho fescue is a desirable bunchgrass found on rangelands of the Pacific Northwest, and is an excellent forage for both livestock and wildlife (Vavra and Sneva 1978; Dragt and Havstad 1987). This native bunchgrass has the potential to be an important component in seed mixtures used in restoring degraded rangelands. However, after-ripening requirements of Idaho fescue, or changes in germinability through time following seed shatter, are not reported in the literature. Knowledge of Idaho fescue's after-ripening requirements in would prove important in reseeding efforts, as the inclusion of dormant and nondormant seed in a mixture will likely
result in the competitive exclusion of the dormant species from the resulting stand
(Simpson 1990; Weiner 1985). I hypothesized that dormancy in Idaho fescue seed
would diminish through time during the first 12 months following seed shatter. I also
wanted to determine the effect of storage temperatures on seed dormancy in Idaho
fescue.

Materials and Methods

The objectives of this experiment were to determine the days to the start of
germination, median response time, Maguire’s (1962) coefficient of the rate of
germination (CRG), and percent germination for Idaho fescue seed of various ages
stored either at room temperature or cooler temperatures that simulated autumn field
conditions. Seeds were collected in central Oregon at a site near McCoin Orchard on
the Crooked River National Grassland. Seeds were hand-stripped in late July 1989,
shortly before seed shatter, and again a year later. Seeds collected in both 1989 and
1990 were used in the 12 month treatments to compare germinability of the seed
crops of the different years, and germinability after 24 months of storage was
investigated using the 1989 seed as well. Both years had less than normal
precipitation, though 1990 was considerably more droughty than 1989 (ch. 2).
Collected seeds were mechanically threshed and a seed blower was used to sort filled
seeds from chaff and unfilled seeds. Seed mass and percent fill were much lower in
1990 than in 1989 (ch. 4).
My hypothesis was tested using a completely randomized experiment with two factors, seed age and storage temperature. Fifty seeds in a plastic germination box constituted an experimental unit. Treatments were as shown in table 5.1. Each treatment was replicated four times. Investigations of after-ripening requirements in seeds should begin at seed maturity and continue for at least six months (Young and

Table 5.1 The 17 treatments used in the investigation of after-ripening requirements in Idaho fescue.

<table>
<thead>
<tr>
<th>Seed Crop Year</th>
<th>Seed Age</th>
<th>Storage Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>Twelve months</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Twenty-four months</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Fresh</td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>Two Weeks</td>
<td>20¹</td>
</tr>
<tr>
<td></td>
<td>Two Weeks</td>
<td>5/15²</td>
</tr>
<tr>
<td></td>
<td>Four Weeks</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Four Weeks</td>
<td>5/15</td>
</tr>
<tr>
<td></td>
<td>Six Weeks</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Six Weeks</td>
<td>5/15</td>
</tr>
<tr>
<td></td>
<td>Eight Weeks</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Eight Weeks</td>
<td>5/15</td>
</tr>
<tr>
<td></td>
<td>Twelve Weeks</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Twelve Weeks</td>
<td>5/15</td>
</tr>
<tr>
<td></td>
<td>Six Months</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>Six Months</td>
<td>5/15</td>
</tr>
<tr>
<td></td>
<td>Twelve Months</td>
<td>20</td>
</tr>
<tr>
<td>1990</td>
<td>Twelve Months</td>
<td>5/15</td>
</tr>
</tbody>
</table>

1. Room temperature storage. 2. Cool temperature storage; 12 hours at each temperature.
Young 1986). I began testing three days after seeds were harvested, and included 12 and 24 month old seed.

I programmed a Hoffman SG-30 germinator (Hoffman Manufacturing Co.) with a temperature regime favorable for germination of Idaho fescue (Doescher et al. 1985; Young and Evans 1982; Young et al. 1981). A 15 °C, 8 hour cool period alternated with a 20 °C, 16 hour warm period, with lights in the germinator on for 12 hours during the warm period. A second Hoffman SG-30 germinator was programmed for alternating 12 hour periods of 5 °C and 15 °C, roughly reflecting mean minimum and maximum field temperatures during the fall (ch. 2), but without lights. Cool-stored seeds were placed in this germinator. Warm-stored seeds were kept at room temperature (about 20 °C). Seeds were stored in paper envelopes and kept dry.

Seeds were germinated on Kimpak* (Seedburo Equipment Co.) moistened with distilled water in transparent acrylic germination boxes (11 x 11 x 3 cm; Hoffman Manufacturing Co.). Seeds were distributed over the substrate so that all seeds were in contact with the moistened substrate. Within a treatment, lots of 50 seeds were randomly assigned to germination boxes, and the boxes randomly assigned to shelves in the germinator with the limitation of a single replicate of any one treatment on any one shelf. Germination boxes were sealed in transparent Ziplock* bags to maintain high humidity. Seeds were not treated with fungicide.

Each germination trial was run for 30 days, and boxes were examined for germinated seeds daily. Germination was defined as the elongation of a radicle or
shoot to 5 mm length, and germinated seeds were removed. After germination commenced, it was considered to have ceased after seven consecutive days with no additional germination. Ungerminated seeds were not removed from germination boxes until the trial was completed.

Germination percentage equalled the number of germinated seeds divided by the total number of filled seeds. Days to germination equaled the number of days that passed before the first seed germinated. Median response time equaled the time required for 50 % of the seeds that ultimately germinated in a particular replicate to have actually done so. The CRG values were calculated as:

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

where \( N_i \) is the number of seeds germinating on the \( i^{th} \) day and \( T_i \) is the \( i^{th} \) day from sowing. The CRG is very sensitive to early responses, as a seed germinating on the first day following sowing carries 30 times the weight of a seed germinating on the 30\(^{th} \) day of a trial. Thus, a high CRG reflects rapid and probably extensive germination whereas a low CRG reflects slower germination, and probably a less complete response. Germination coefficients such as CRG have been criticized for confounding the effects of time of response and number of seeds responding (Scott et al. 1984; Brown and Mayer 1986). However, because early emergence confers substantial advantages to seedlings in a competitive environment (Ross and Harper 1972; Weiner 1985), CRG retains interpretable ecological significance at the level of the population.
Statistical analyses of the experiments were made using Number Cruncher Statistical System™ (Hintze 1990, 1992). For each population within an experiment, results were tested and plotted to determine normality and equality of variance. Normality was tested using D'Agostino's univariate normality tests (α = 0.01), which include skewness and kurtosis tests and an omnibus normality test, along with normal probability plots using 95% confidence limits. Equality of variance was tested using the Bartlett-Box homogeneity test (α=0.01). The T² multivariate outlier test (α=0.01) was used to test for outliers.

Two response variables failed to satisfy assumptions underlying ANOVA. Days-to-germination was not normally distributed for two-week old seeds, and the variance of median response times was heterogeneous. Log (base e) transformations of these variables, and the remaining response variables (percent germination, loss to fungi, and CRG), passed the normality, outlier, and homogeneity of variance tests.

Data from the 1990 seeds were analyzed using two-factor ANOVA and a separate analysis was run for each response variable. Because fresh seed was not stored at any temperature prior to germination, this treatment was not included in the two-way ANOVA's. When seed age was a significant factor, a one-way ANOVA for this factor was run that included all treatments, and means were separated using Fisher's Protected LSD (α=0.05). Differences between 1989 and 1990 seeds and between 12 and 24 month old 1989 seeds were tested using one-tailed t-tests (α=0.05). In the cases of the transformed variables, untransformed means are reported with differences determined using the transformed data.
Results

Germination of 1990 seeds increased with seed age (time since harvest) (F=15.83, p<0.000) during the first six months of storage (fig. 5.1). Only 35 % of fresh seeds germinated, significantly fewer than in any other treatment. With two to eight weeks of after-ripening, about half the seeds had broken dormancy and germinated. Germination increased to 80 % after six months of storage, but dropped to 58 % after 12 months. Storage temperature (F=0.05, p=0.827) did not have a significant influence on percent germination of 1990 seeds. Germinability was much greater in 1989 seeds. After 12 months of storage, 95 % of the 1989 seeds germinated compared to 58 % in 1990 seeds of the same age (t=-6.50, p<0.000), and germination of the six-month old 1990 seeds was also significantly poorer compared to six-month old 1989 seeds (t=-2.83, p=0.009). After 24 months of room temperature storage, germination of 1989 seed dropped to 89 %, a significant decline from 12 month old seed (t=3.75, p=0.011). Percent germination did not differ between two-year old 1989 seeds and six-month old 1990 seeds (t=-1.75, p=0.056).

As in total germination, seed age (F=21.33, p<0.000) proved significant in susceptibility to fungal pathogens but storage temperature did not (F=0.03, p=0.868). Seed destruction by fungi was greatest in the fresh seed treatment (fig. 5.2), which had the lowest percent germination. Among the 1990 seed, losses to fungi were lowest among the seeds which had after-ripened for 6 months. Many
seeds were destroyed by fungi in all treatments using 1990 seeds. Losses ranged from 54 % in fresh seeds to 13 % in six month old seeds. In general, failure to germinate meant destruction by fungi. The 1989 seeds were much more resistant to fungal attack. Only 1.5 seeds were, on average, lost to fungi in treatments using 12 month old 1989 seed, compared to 12.1 for 1990 seeds of the same age ($t=4.97$, $p<0.000$). The number of seeds lost rose to 3.5 seeds when after-ripened for 24 months, but the difference between one and two years of after-ripening was not significant ($t=-1.73$, $p=0.067$). In comparison, the treatment using 1990 seeds

![Figure 5.1 Effect of after-ripening on germination of Idaho fescue seed produced during a dry year.](image)
which showed the greatest resistance to fungal attack was 6 month old seed. This treatment averaged 6.6 seeds destroyed by fungi, which was significantly greater than in 12 month old 1989 seed \((t=2.47, p=0.017)\). After two years of after-ripening, 1989 seeds were as susceptible to decay as were the six month old 1990 seeds \((t=1.55, p=0.077)\).

The rapidity with which germination commenced in the 1990 seeds depended upon the interaction of seed age and storage temperature \((F=4.07, p=0.003)\). Seeds which had been stored at room temperature tended to germinate slightly sooner than
did seeds stored at cooler alternating temperatures (table 5.2). However, the difference, 5.1 versus 5.6 days, is probably not biologically significant. Interestingly, seeds that had been stored at cool alternating temperatures (5/15 °C) and after-ripened for four weeks or less began germinating slightly sooner than seeds of the same age which had been stored at room temperature (20 °C); the pattern was reversed once seeds had after-ripened for at least six weeks. The delay to the start of germination tended to shorten as the period of after-ripening was increased. Fresh seeds were much slower to begin germinating than were seeds which had after-ripened even for a short period. Seeds that had after-ripened the longest were the quickest to begin germinating, particularly if stored at room temperature. There were no differences between 1990 and 1989 seed in days to germination for seeds aged 6 months or greater, and 24 month old seeds began germinating as quickly as 12 month old seeds from the same lot.

Table 5.2 Two-way interaction means for days to initial germination of 1990 Idaho fescue seed.

<table>
<thead>
<tr>
<th>Storage Temp. (C)</th>
<th>0</th>
<th>2</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>12</th>
<th>26</th>
<th>52</th>
<th>Mean²</th>
</tr>
</thead>
<tbody>
<tr>
<td>5/15</td>
<td>5.00</td>
<td>5.75</td>
<td>6.50</td>
<td>6.00</td>
<td>6.00</td>
<td>5.00</td>
<td>5.00</td>
<td>5.63a</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>5.75</td>
<td>6.25</td>
<td>5.50</td>
<td>5.00</td>
<td>5.25</td>
<td>4.50</td>
<td>3.75</td>
<td>5.14b</td>
<td></td>
</tr>
<tr>
<td>Mean¹</td>
<td>7.75a</td>
<td>5.38bc</td>
<td>6.00b</td>
<td>6.00b</td>
<td>5.50b</td>
<td>5.63b</td>
<td>4.75cd</td>
<td>4.38d</td>
<td></td>
</tr>
</tbody>
</table>

Within a row or column, different letters indicate significant differences (α=0.05). 1. n=8 and se=0.2494 for all seed age means except for fresh seeds where n=4 and se=0.3527. 2. n=28 and se=0.1041.
The rate of germination also depended upon the interaction of seed age and storage temperature \((F=2.99, p=0.016)\), though both factors exercised a strong influence \((\text{seed age: } F=33.51, p<0.000; \text{ storage temperature: } F=35.50, p<0.000)\).

Storage at cool alternating temperatures resulted in slower germination, and increasing the period of after-ripening tended to speed germination (table 5.3). The median response was attained with equal speed in all treatments where seeds had been after-ripened six or more months, irrespective of year of production, and these treatments had the shortest median response times.

Table 5.3 Two-way interaction means for median response times of 1990 Idaho fescue seed.

<table>
<thead>
<tr>
<th>Storage Temp. (C)</th>
<th>Seed Age (Weeks)</th>
<th>Mean²</th>
</tr>
</thead>
<tbody>
<tr>
<td>5/15</td>
<td>0  2  4  6  8  12 26 52</td>
<td></td>
</tr>
<tr>
<td>11.50</td>
<td>10.25</td>
<td>12.00</td>
</tr>
<tr>
<td>11.50</td>
<td>9.25</td>
<td>8.25</td>
</tr>
<tr>
<td>11.25</td>
<td>10.00</td>
<td>9.25</td>
</tr>
<tr>
<td>20</td>
<td>6.75</td>
<td>6.25</td>
</tr>
<tr>
<td>Mean¹</td>
<td>12.3a</td>
<td>11.4a</td>
</tr>
<tr>
<td></td>
<td>10.1bc</td>
<td>7.0d</td>
</tr>
</tbody>
</table>

Within a row or column, different letters indicate significant differences \((\alpha=0.05)\). 1. \(n=8\) and \(se=0.4788\) for all seed age means except for fresh seeds where \(n=4\) and \(se=0.6772\). 2. \(n=28\) and \(se=0.1827\).

The interaction of seed age and storage temperature \((F=2.54, p=0.034)\) significantly influenced CRG values, but the most influential factor, by far, was seed age \((F=48.38, p<0.000)\). Storage at cool temperatures tended to give lower CRG values (table 5.4). Lengthening the period of after-ripening promoted higher CRG's until seeds had been in storage for 6 months. Seeds which had after-ripened for eight weeks or less had CRG values between 1.393 and 2.131. Six months of after-
ripening resulted in a dramatic increase in the CRG to 5.529, but with 12 months of storage the CRG dropped just as dramatically. Seeds collected in 1989 gave higher CRG’s than any treatment using 1990 seed. The CRG of 12 month old 1989 seed (6.571) was over twice that of 1990 seed of the same age (t= -10.15, p<0.000), and was significantly greater than that of the six month old 1990 seeds (t= -2.69, p=0.011). Twenty-four month old 1989 seeds also had a greater CRG than the six month old 1990 seeds (t= -2.76, p=0.010). The CRG’s of 1989 seeds, whether after-ripened 12 or 24 months, were the same (t= -0.31, p=0.385).

Table 5.4 Two-way interaction means\(^1\) for CRG of 1990 Idaho fescue seed.

<table>
<thead>
<tr>
<th>Storage Temp. (C)</th>
<th>Seed Age in Weeks</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>5/15</td>
<td>2.19</td>
<td>1.61</td>
</tr>
<tr>
<td>20</td>
<td>2.07</td>
<td>2.26</td>
</tr>
<tr>
<td>Mean</td>
<td>1.39a</td>
<td>2.13b</td>
</tr>
</tbody>
</table>

Within a row or column, different letters indicate significant differences (\(\alpha=0.05\)). 1. \(n=8\) and \(se=0.2038\) for all seed age means except for fresh seeds where \(n=4\) and \(se=0.2882\). 2. \(n=28\) and \(se=0.0099\).

Discussion

Idaho fescue seed crops, like most grasses, include dormant and nondormant seeds. I found about \(\%\) of the seeds to be dormant at dispersal, with six months of after-ripening resulting in loss of dormancy. I did not, however, determine the cause of dormancy.
When compared to climatological patterns, the patterns of dormancy in Idaho fescue seed reveal adaptation to the rangeland environment. Idaho fescue seeds mature during summer and seed shatter occurs in late July and early August – the driest time of the year. August receives the least precipitation (9 mm) and has the warmest temperatures (18.7 °C), on average, of any month (Anon. 1983). Prompt germination following seed dispersal would very likely result in desiccation and death. Newly emerged seedlings would be entirely dependent upon rainfall in the late summer, because plant growth during spring and summer would have depleted stored soil moisture. Germination in late summer or early fall frequently results in the death of the majority of rangeland grass seedlings (Pyke 1990; Harris 1967; Weaver and Mueller 1942). In Idaho fescue, 70% of the seed crop is dormant at this time.

The autumn months offer improved moisture relations, but temperatures are cool. September, for example, averages 16.4 mm of precipitation and a temperature of 13.4 °C. October and the following months are wetter and cooler. Two months following seed shatter in Idaho fescue, over half the seed crop remains dormant. Greater than 50 % of annual precipitation is delivered during the November to March period, either as snow or low intensity rain storms that allow most of the moisture to infiltrate the soil (Anon. 1983; West 1988). By February, six months after seed shatter, a seedling faces a much lower risk of desiccation and a higher probability of survival. After-ripening requirements in Idaho fescue seed result in the greatest potential germination coinciding with the time of year most favorable for seedling establishment.
There is, however, a second dimension to the relationship of seed dormancy and climate that allows nondormant seeds to be potentially adaptive. Weather in rangelands is highly variable, both spatially and temporally (Hidy and Klieforth 1990). For example, standard deviations associated with mean precipitation for August, September, and October roughly equal the means (see ch. 2). Occasionally, August is wet; environmental conditions that are favorable for germination and establishment are possible any time of year. On these infrequent occasions, nondormant seeds offer the potential for seedling establishment.

Both 1989 and 1990 were drier than average, with 90 % of normal precipitation falling in 1989 but only 60 % of normal in 1990. More importantly, precipitation delivered during the March through July period, when the maternal plant would have resumed growth after winter dormancy, elevated inflorescences, and filled seed, was 145 % of normal in 1989 and 94 % of the long-term average in 1990. Water relations are very important in seed production by rangeland grasses as the carbon allocated to sexual reproduction is derived from concurrent photosynthesis rather than translocation from storage organs (Briske 1991; Caldwell et al. 1981; Moser 1977). Suitable water relations are required for gas exchange in photosynthetic tissues and cell expansion in the developing seed. Conditions were more favorable for seed production in 1989 than in 1990.

Water relations of the maternal plant strongly influence seed dormancy in other grasses with dry, warm conditions during grain filling resulting in reduced seed dormancy (Benech Arnold et al. 1991, 1992; Nelson and Wilson 1969; Shaidaee et al.
This may help explain the marked variation in longevity of seeds produced under conditions of differing soil moisture availability observed in this study. With six months of after-ripening, the 1990 seed crop achieved 80% germination, but by 12 months, germination had dropped to 58%. Twelve-month old seed produced in 1989 achieved 95% germination under the same conditions, and 89% of the seeds germinated after two years of storage. I believe this difference in longevity is due to water relations of the maternal plant during flowering and grain filling. Seed mass and percent fill were significantly greater in the 1989 crop compared to 1990 (see ch. 3). Droughty conditions in 1990 resulted in fewer seeds being produced, and those that were, were poorly filled. The 1990 seeds proved more susceptible to fungal attack than the 1989 seeds as well. Young and Young (1986) argue that normal, healthy seeds are generally able to resist fungal pathogens.

The temperatures at which Idaho fescue seeds were after-ripened did not affect total germination, but did influence the rate of germination. Seeds after-ripened at room temperature tended to begin germinating earlier than seeds after-ripened in a regime of cooler, alternating temperatures that roughly simulated autumn field conditions. Seeds stored at room temperature also maintained a higher rate of germination during the test. These trends are typical of grasses: storage of dry seed at low temperature enforces dormancy (Simpson 1990).

My results suggest that rangeland managers attempting to improve degraded rangelands by seeding Idaho fescue should collect seed in wet years (when the quantity of seed would also be greatest), should after-ripen the seed for six months
before sowing, and should use the seed within two or three years of harvest for best results. Storage at cool temperatures (5 °C) will lengthen the period during which seeds can be stored with little loss of viability. Wasser (1982) suggests planting Idaho fescue seed at a depth of 1.2 cm, and long-term climate records suggest early spring as the time most likely to result in successful stand establishment.

Literature Cited


CHAPTER VI. ROOT AND SHOOT GROWTH OF IDAHO FESCUE AND CHEATGRASS

Jay R. Goodwin, Paul S. Doescher, and Lee E. Eddleman
Competitive ability is a function of the area, the activity, and the distribution in space and time of the plant surfaces through which resources are absorbed

J.P. Grime (1979:9)
Plant growth is most limited by the availability of soil resources, especially water, on Intermountain rangelands of the western U.S. (Smith and Nowak 1990; Eissenstat and Caldwell 1988, 1989; Fowler 1986; Ries and Fisser 1979). Because precipitation falls primarily during winter, growth by western rangeland grasses is dependent upon moisture stored in the soil profile (Cline et al. 1977). Access to this moisture controls plant growth, survival, and reproduction, and the ability to capture soil moisture is a measure of competitiveness in this system (Eissenstat and Caldwell 1988). Individuals that take up and transpire this moisture prevent its use by other plants, and the quantity of moisture available for growth is limited.

A critical factor in a plant's ability to take up soil moisture is the quantity and distribution of absorptive root surface area and transpiring shoot surface area (Larcher 1991; Fitter and Hay 1987). The greater the amount of absorptive root surface, the greater the rate at which moisture can be absorbed. The greater the transpiring surface area, the greater the rate at which water can leave the plant, which will in turn result in a steeper water potential gradient. Thus, both leaf area and root length are important attributes when investigating the ability of rangeland grasses to compete for soil moisture.

Plant allocation patterns often reveal a tendency to produce more of the surface which absorbs the resource most limiting growth (Larcher 1991; Fitter and Hay 1987), and the majority of plant biomass is belowground in semiarid grasslands
Because of its root phenology and morphology, cheatgrass is a very effective competitor for soil moisture (Harris 1967, 1977; Harris and Wilson 1970; Cline et al. 1977; Melgoza et al. 1990). Cheatgrass roots grow during winter and rapid shoot growth occurs during a brief period in spring. In contrast, growth rates are slower in native perennial bunchgrasses, and active spring growth starts later compared to cheatgrass. When a native bunchgrass has cheatgrass for a neighbor, the native is subject to greater water stress earlier in the season (Melgoza et al. 1990; Harris and Goebel 1976). Seedlings of native bunchgrasses face an even worse situation as they enter spring with a poorly-developed root system.

In this study, I sought to determine whether root and shoot growth in populations of Idaho fescue which persist on degraded Oregon rangelands could explain their persistence. Rapid and efficient root and shoot production could confer greater competitive ability. In order to compete with cheatgrass for soil moisture, Idaho fescue would have to send roots down into the soil profile at a rate comparable to that of cheatgrass, and produce the leaf area required for a comparable water potential gradient. Otherwise, Idaho fescue roots would be left in soil at or near the permanent wilting point as the faster growing cheatgrass exploited stored moisture (Harris 1967; Harris and Wilson 1970; Reichenberger and Pyke 1990).

I examined root growth in Idaho fescue seedlings from an undisturbed site (the Island (Driscoll 1964)) and four disturbed sites which have been grazed by cattle and invaded by cheatgrass. Cheatgrass seedlings were included to allow comparison. I
hypothesized that Idaho fescue persisting on degraded sites would have faster root and shoot growth, with roots reaching greater depths and shoots having greater leaf area, than seedlings from the relict population. The hypotheses tested in this experiment were that root and shoot growth rates, and specific root length and specific leaf area, would be greater in seedlings from disturbed sites compared to seedlings from a relict population, and that rates of root growth would be similar in cheatgrass seedlings and Idaho fescue seedlings from disturbed sites. The null hypotheses were that there would be no differences. The objectives in this investigation were to determine rooting depth, root length density, specific root length, specific leaf area, and allocation patterns in the three groups (disturbed and undisturbed Idaho fescue, and cheatgrass).

Materials and Methods

I tested the hypotheses using a completely randomized design. Seedlings of Idaho fescue and cheatgrass were grown in a greenhouse in a double tube assembly: a soil-filled glass inner tube (51 mm x 122 cm) and a black PVC tube of slightly larger diameter which protected the glass tube from breakage and provided a dark soil column. The soil-filled tubes slid out of the protective tubes for root observation. The tube assemblies were supported in a wooden frame which held each tube inclined at an angle of 17° to allow nondestructive root growth measurements along the side of
the tube (Harris 1967). A soil-filled glass tube containing an individual seedling constituted an experimental unit.

Glass tubes were filled with soil from Combs Flat in a manner that duplicated the indigenous soil profile. A pit 1.2 m deep was dug and the excavated soil separated by strata; soil from the lowest stratum was added to the glass tube first and surface soil was added last. The soil was not amended or sterilized in any way. The bottom ends of the glass tubes were plugged using a rubber stopper with a drain hole. Soil was brought to field capacity two weeks before seeds were planted. Any seedlings that emerged prior to planting were removed.

The same collections of seed were used in this experiment as were used in the germination experiment described previously (ch. 3). Seeds of the five collections of Idaho fescue and the McCoin collection of cheatgrass were used. Five replicate seedlings of each collection were employed in the experiment, requiring 30 glass tubes (six accessions (five of Idaho fescue and one of cheatgrass) with five replicates each). Replicates were randomly assigned to tubes, and tubes were randomly assigned to positions in the frame. Three seeds were planted 5 mm below the soil surface in each replication. Because cheatgrass germinates more rapidly than Idaho fescue (Hull 1973; Doescher et al. 1985), cheatgrass seeds were planted four days after Idaho fescue seeds to more closely group time of emergence. Idaho fescue was planted on 7 January and cheatgrass on 11 January. Tap water (roughly 50 ml) was added to the tubes at the time of planting, with subsequent watering once a week to prevent water stress (wilting) in the seedlings. If multiple seedlings emerged, extras
were removed. If no seedlings emerged, or if a seedling died shortly after emergence, one was transplanted from another replication of the same treatment having an excess. Harvest dates were adjusted to allow an equal period of growth for all seedlings.

The experiment ran for 60 days, with alternating day/night temperatures of 24 and 18 °C in the greenhouse. Ambient daylight was supplemented by florescent tubes giving a photosynthetic photon flux density of 205.6 μE/m/s. Lights were on for 14 hours in every 24 to simulate spring day length. Temperatures in the glass root tubes were monitored on a weekly basis using thermocouples at depths of 5, 15, 25, 50, 75, and 100 cm. Despite being in a greenhouse, a temperature gradient existed in the root tubes. At a depth of 5 cm, soil temperature averaged 23 °C and dropped to 16 °C at 100 cm during the day (fig. 6.1).

![Figure 6.1 Soil temperature gradient in the root tubes during daylight.](image)
Rooting depth, shoot height, and number of leaves were recorded once a week over the course of the experiment. Rooting depth equaled the distance from the germinated seed to the lowest root tip. Because internodal elongation is limited to reproductive culms in Idaho fescue, shoot height was measured as the vertical distance from the soil surface to the tip of the longest leaf.

After 60 days, seedlings were harvested. When possible, 10 fully-expanded leaves were collected to determine mean leaf area; all leaves were used when fewer than 10 had been produced. Only the leaf blade from collar to leaf tip was used. Leaf area was calculated on the basis of leaf geometry: surface area of a triangle for cheatgrass and surface area of a cone for Idaho fescue. Length and width measurements were made using a transparent ruler and, for width of Idaho fescue, a microscope with graduated eyepiece. Total plant leaf area was calculated by multiplying mean leaf area by the number of leaves produced.

Roots were separated from soil by soaking the soil-filled tube in a water bath for 12 hours and subsequently elevating the bottom end of the tube while still in the bath. The wet soil column slid easily from the tube onto plastic screening, allowing harvest of an intact root system in most cases. The root system was then briefly cleaned of soil particles and foreign organic matter by gently shaking the screen in the bath, then transferred to another water bath. Extracted root systems were soaked for an additional 12 hours, cleaned, and after drying at room temperature for ½ hour, weighed. Roots were partitioned by soil stratum (0-2, 2-5, 5-10, 10-20, 20-50, 50-120 cm).
Within a stratum, individual root segments were teased apart in a water bath. Three root samples were randomly selected from each stratum and length and mass measured. In some cases, particularly at depths of greatest penetration, only one or two root segments were available. The length of a root segment was determined by measuring the length of the primary root axis and then increasing this length to reflect the contribution to total segment length made by fine (≤0.3 mm) laterals. The proportion of the root segment's length contributed by fine lateral roots was visually estimated. Total root length was then calculated from the mean length per unit mass of samples. Harvested root, leaf, and shoot material was dried at 50 °C and weighed. Total leaf area, specific leaf area, specific root length, root length density, root weight:plant weight and root length:leaf area ratios were calculated.

The experiment yielded variables that could be analyzed using one-way ANOVA (total root length, root length density, and root mass, leaf area, specific leaf area, shoot mass, and root weight:plant weight and root length:leaf area ratios), two-way ANOVA (root biomass distribution in the soil column), and variables which required repeated measures ANOVA (rooting depth, leaf length, and number of leaves). Number Cruncher Statistical System™ (NCSS) (Hintze 1990, 1992) was used for the one- and two-way ANOVA’s, but Statistical Analysis System™ (SAS 1987) was required for the repeated measures ANOVA’s because of missing values. The general linear model procedures for ANOVA were used in both programs. The Curve Fitter module of NCSS (Hintze 1991) was used to determine an allometric constant for shoot and root allocation in Idaho fescue.
For each population, results were tested and plotted to determine conformance to ANOVA assumptions. Logarithmic (base e) transformations were required of root length, root length density, and number of leaves before these variables satisfied ANOVA assumptions. The remaining response variables passed normality, outlier, and homogeneity of variance tests. Differences between the undisturbed (Island) and disturbed Idaho fescue populations were tested using contrasts. To allow comparison with cheatgrass when a transformation was required, untransformed means are reported with differences determined using log transformed data. Because of missing observations, data from week one were excluded from the analyses of rooting depth and shoot height. In the analysis of Idaho fescue root distribution, the deepest stratum (50-120 cm) was excluded because only four seedlings extended roots to depths greater than 50 cm. Given a significant F-test, differences among the individual populations were determined using Fischer’s Protected LSD. The significance level for all tests was 0.05.

In many cases, means for cheatgrass were many times greater than that of any Idaho fescue population, and differences among the Idaho fescue populations could not be detected when cheatgrass was included in the analysis. Because the focus of this research was variation among the Idaho fescue populations, cheatgrass was excluded from the analysis in these cases.
Results

Seedlings from the disturbed Idaho fescue populations were slower to emerge than were Island seedlings (table 6.1). Island seedlings emerged seven days after planting while seedlings from the disturbed populations required 11 days for emergence (F = 7.90, p < 0.05). Among the Idaho fescue populations, Mc Coin seedlings were the slowest to emerge (fig. 6.2). Emergence was quickest among Island and Blanchard seedlings. Cheatgrass seedlings emerged only 4.8 days after sowing.

Table 6.1 Size and allocation patterns in Idaho fescue seedlings of populations from disturbed and undisturbed sites.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Undisturbed¹</th>
<th>Disturbed²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
</tr>
<tr>
<td>Emergence (days)</td>
<td>7.00a</td>
<td>1.310</td>
</tr>
<tr>
<td>Total Root Length (cm)</td>
<td>963.32a</td>
<td>158.098</td>
</tr>
<tr>
<td>Specific Root Length (cm/g)</td>
<td>33354.14a</td>
<td>8061.327</td>
</tr>
<tr>
<td>Root Length Density (cm/cm³)</td>
<td>1.07a</td>
<td>0.185</td>
</tr>
<tr>
<td>Mean Rooting Depth (cm)⁵</td>
<td>21.79a³</td>
<td>1.630</td>
</tr>
<tr>
<td>Mean Shoot Height (cm)⁵</td>
<td>9.28a³</td>
<td>1.792</td>
</tr>
<tr>
<td>Mean Number of Leaves⁵</td>
<td>5.16a⁴</td>
<td>1.160</td>
</tr>
<tr>
<td>Total Leaf Area (cm²)</td>
<td>11.66a</td>
<td>1.468</td>
</tr>
<tr>
<td>Specific Leaf Area (cm²/g)</td>
<td>231.86a</td>
<td>21.993</td>
</tr>
</tbody>
</table>

Within a row, different letters indicate significant differences (α = 0.05). ¹. n=4 ². n=19 ³. Undisturbed n=7, Disturbed n=28. ⁴. Undisturbed n=8, Disturbed n=32. ⁵. Average for the eight weeks of the experiment; see text for depth, height, and number after eight weeks growth.
Rooting depth was different for the disturbed and undisturbed Idaho fescue populations (table 6.1; \( F=12.44, \ p=0.0006 \)), though this was largely due to poor root growth in one of the four disturbed-site populations. Island seedlings had an average rooting depth 3 cm greater than the disturbed-site seedlings. However, this difference is unlikely to be biologically significant. Island seedlings extended roots to a depth of 39.2 cm in eight weeks (fig. 6.3). Of the four disturbed-site populations, Lone Pine seedlings consistently had the slowest root growth and shallowest roots, reaching 29.5 cm by the end of the experiment. Blanchard seedlings rooted to 32.8 cm, slightly deeper than Lone Pine. Combs Flat and Mc Coin seedlings had similar rooting depths at the end of the experiment, 36.7 and 36.4 cm, respectively. Seedling
Figure 6.3 Root extension by seedlings of five Idaho fescue populations.

root growth was much faster in cheatgrass than in Idaho fescue (table 6.2), with roots reaching a depth of 119.6 cm after 60 days.

Shoot height was also greater in Island seedlings than in the seedlings from disturbed sites (table 6.1; F=69.60, p=0.0001). Over the entire experiment, Island seedlings had an average height 2.3 cm taller than the disturbed-site seedlings. Leaves of Island seedlings consistently grew the fastest and reached a height of 12.4 cm in eight weeks (fig. 6.4). Among the Idaho fescue populations from disturbed sites, Blanchard had the shortest shoots (8.4 cm) at the end of the experiment. Combs Flat, Lone Pine, and McCoin had intermediate heights (9.1, 10.3, and 9.6 cm,
Table 6.2 Size and allocation patterns in cheatgrass seedlings.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emergence (days)</td>
<td>4.80</td>
<td>1.310</td>
</tr>
<tr>
<td>Total Root Length (cm)</td>
<td>16348.88</td>
<td>769.429</td>
</tr>
<tr>
<td>Specific Root Length (cm/g)</td>
<td>18704.17</td>
<td>1265.890</td>
</tr>
<tr>
<td>Root Length Density (cm/cm³)</td>
<td>6.69</td>
<td>0.306</td>
</tr>
<tr>
<td>Mean Rooting Depth (cm³)</td>
<td>68.07²</td>
<td>6.146</td>
</tr>
<tr>
<td>Mean Shoot Height (cm³)</td>
<td>23.31²</td>
<td>1.538</td>
</tr>
<tr>
<td>Mean Number of Leaves³</td>
<td>11.95²</td>
<td>1.731</td>
</tr>
<tr>
<td>Total Leaf Area (cm²)</td>
<td>125.42</td>
<td>6.266</td>
</tr>
<tr>
<td>Specific Leaf Area (cm²/g)</td>
<td>226.40</td>
<td>9.229</td>
</tr>
<tr>
<td>Root Biomass (g)</td>
<td>0.89</td>
<td>0.073</td>
</tr>
<tr>
<td>Shoot Biomass (g)</td>
<td>0.71</td>
<td>0.044</td>
</tr>
<tr>
<td>Root Weight Ratio</td>
<td>0.55</td>
<td>0.033</td>
</tr>
<tr>
<td>Root Length:Leaf Area (cm²/cm²)</td>
<td>132.52</td>
<td>12.295</td>
</tr>
</tbody>
</table>

1. n=5  2. n=40  3. Average for the eight weeks of the experiment; see text for depth, height, and number after eight weeks growth.

respectively). Cheatgrass was taller than Idaho fescue, reaching 31.1 cm after 60 days growth.

Island seedlings averaged 1.5 more leaves than seedlings from the disturbed sites over the entire experiment (table 6.1; F=14.53, p=0.0002). The Combs Flat, Lone Pine, and McCoin populations produced the fewest leaves, with 7.8, 8.6, and 6.2 leaves, respectively, after eight weeks growth (fig. 6.5). Island seedlings had 12.4 leaves at the end of the experiment, and Blanchard seedlings had 10. Cheatgrass
Figure 6.4 Shoot growth in five Idaho fescue seedling populations.

Figure 6.5 Leaf production by seedlings of five Idaho fescue populations.
averaged more than twice as many leaves as the Island seedlings (table 6.2), and had 29.6 leaves after eight weeks growth.

Total root length ($F=8.61$, $p<0.05$) was roughly three times greater in Island seedlings compared to seedlings from the disturbed populations (table 6.1). The Combs Flat, Lone Pine, and McCoin Idaho fescue populations produced less root length than the Island and Blanchard populations (fig. 6.6). The same pattern was evident in leaf area ($F=25.84$, $p<0.05$) for the two groups (table 6.1). There were no differences among the disturbed site populations in leaf area (fig. 6.7). In contrast, cheatgrass averaged more than ten times the root length and leaf area of Island Idaho fescue (table 6.2).

Figure 6.6 Total root length after 60 days growth for seedlings of five Idaho fescue populations.
Island seedlings had twice the root density of disturbed site seedlings ($F=7.80$, $p<0.05$) (table 6.1). Differences in root density among the disturbed-site populations were not significant (fig. 6.8). The root density of cheatgrass was six-fold greater than that of any Idaho fescue population.

Both root ($F=25.33$, $p<0.05$) and shoot ($F=45.64$, $p<0.05$) biomass were considerably greater in Island seedlings than in seedlings from the disturbed populations (table 6.3). There were no differences in root or shoot biomass among the disturbed-site seedlings. Cheatgrass biomass, both root and shoot, was much greater than that of Idaho fescue (table 6.2).
Though Island seedlings had greater root and shoot biomass, allocations to root and shoot were of the same proportions in the two Idaho fescue groups. The disturbed-site and Island seedlings had similar root weight ratios, which express the proportion of total biomass in roots (table 6.3; $F=0.58$, $p>0.05$). In the Idaho fescue seedlings, roots accounted for roughly 31% of total plant biomass. Root length:leaf area ratios were also the same for the two Idaho fescue groups (table 6.3; $F=0.00$, $p>0.05$). The allometric constant for Idaho fescue allocation patterns was 0.9127 ($r^2=0.76$). Allocation to roots was much greater in cheatgrass, with 55% of plant biomass in roots (table 6.2). The root length:leaf area ratio of cheatgrass was roughly double that of Idaho fescue.
Table 6.3 Root and shoot biomass of Idaho fescue seedlings from populations found on disturbed and undisturbed sites.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Undisturbed</th>
<th>Disturbed</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SE</td>
<td>Mean</td>
</tr>
<tr>
<td>Root Biomass (g)</td>
<td>0.0279a</td>
<td>0.004</td>
<td>0.0085b</td>
</tr>
<tr>
<td>Shoot Biomass (g)</td>
<td>0.0712a</td>
<td>0.007</td>
<td>0.0177b</td>
</tr>
<tr>
<td>Root Weight Ratio</td>
<td>0.2856a</td>
<td>0.048</td>
<td>0.3258a</td>
</tr>
<tr>
<td>Root Length:Leaf Area (cm/cm²)</td>
<td>78.9066a</td>
<td>20.549</td>
<td>79.3394a</td>
</tr>
</tbody>
</table>

Within a row, different letters indicate significant differences (α=0.05). 1. n=4 2. n=19

The distribution of root biomass in soil varied with both group and strata in Idaho fescue seedlings (F=3.09, p=0.013). Island seedlings had greater root biomass at all soil strata than the disturbed-site seedlings, and allocation patterns were different among the two groups (table 6.4). On a per cm basis, root biomass decreased with depth in both groups, though more rapidly in Island seedlings. Sixty-five percent of the root biomass produced by Island seedlings was in the upper 10 cm of the soil column, and the disturbed-site seedlings had 59% of their root biomass in this zone. In contrast to Idaho fescue, cheatgrass invests in deeply penetrating roots. Nearly 60% of cheatgrass root biomass was at depths greater than 10 cm. Cheatgrass root biomass also did not consistently decline with increasing depth. On a per centimeter basis, cheatgrass root biomass was greatest in the upper two cm of the soil column, declined over the next three cm, then increased over the next five cm. Cheatgrass root biomass declined with increasing depth at depths greater than 10 cm.
Table 6.4 Comparison of Idaho fescue and cheatgrass root biomass (mg) by soil column depth (cm).

<table>
<thead>
<tr>
<th>Strata</th>
<th>Idaho fescue</th>
<th>Disturbed</th>
<th>Cheatgrass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Undisturbed</td>
<td>Disturbed</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean(^1)</td>
<td>Mean(^2)</td>
<td>Mean(^3)</td>
</tr>
<tr>
<td>0-2</td>
<td>8.000a</td>
<td>1.788a</td>
<td>136.833bc</td>
</tr>
<tr>
<td>2-5</td>
<td>4.566b</td>
<td>1.564a</td>
<td>88.933c</td>
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<tr>
<td>5-10</td>
<td>6.366ab</td>
<td>1.94a</td>
<td>186.800ab</td>
</tr>
<tr>
<td>10-20</td>
<td>7.700a</td>
<td>2.200a</td>
<td>156.800b</td>
</tr>
<tr>
<td>20-50</td>
<td>3.866b</td>
<td>1.314a</td>
<td>181.333ab</td>
</tr>
<tr>
<td>50-120</td>
<td>0.410c</td>
<td>0.300a</td>
<td>216.823a</td>
</tr>
</tbody>
</table>

\(^{1}\) 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. Different letters within a column represent significant differences (α=0.05) determined through one-way ANOVA for each group.

Reflecting greater allocation to roots, cheatgrass root biomass was many times greater than Idaho fescue root biomass in every stratum.

Among the Idaho fescue populations, Combs Flat, McCoin, and Lone Pine averaged the lowest root biomass across all strata (fig. 6.9). Blanchard seedlings had significantly greater mean root biomass per strata than the other disturbed-site seedlings.

Discussion

Plant growth and metabolic processes are detrimentally affected by even mild water stress (Larcher 1991; Fitter and Hay 1987). Fitter and Hay (1987:132) stated, “it is crucially important for all terrestrial species either to avoid water stress or to
Figure 6.9 Root biomass distribution by soil strata for five Idaho fescue populations.

evolve anatomical, morphological, and biochemical adaptations which lead to the amelioration or tolerance of water stress." This experiment investigated the morphology of Idaho fescue seedlings from a relict population and from populations growing on sites invaded by cheatgrass, and of cheatgrass seedlings. I sought evidence of adaptations that could explain the persistence of Idaho fescue on sites invaded by the highly competitive alien. Soil moisture is the resource which most limits plant growth, survival, and reproduction on central Oregon rangelands (Smith and Nowak 1990; Ries and Fisser 1979), and cheatgrass is a very effective competitor
for soil moisture (Harris 1967; Melgoza et al. 1990). Once the readily available water in the immediate vicinity of a root is depleted, a plant must extend roots into still moist strata and produce more root surface area to continue water uptake (Larcher 1991).

Island seedlings emerged earlier than seedlings from the disturbed sites, thereby gaining a head start in the race to put down roots and take up soil moisture. This initial advantage could have been overcome if the disturbed-site seedlings had greater growth rates than Island seedlings, but they did not. Island seedlings extended roots down the soil column faster than the disturbed-site seedlings and produced $3\frac{1}{2}$ times the root length. Cheatgrass seedlings emerged well ahead of Idaho fescue. Early-emerging seedlings generally out-compete and out-grow seedlings that emerge later (Weiner 1985; Romo and Eddleman 1987; Harris 1977; Ross and Harper 1972), and on Intermountain rangelands, root phenology is of great importance in the competition for stored soil moisture (Harris and Wilson 1970; Harris 1977; Jordan 1983). Under field conditions, Idaho fescue would have to sustain a higher rate of growth than cheatgrass to remain an effective competitor for soil moisture (Reichenberger and Pyke 1990).

Of the two Idaho fescue groups, Island seedlings bore greater resemblance to cheatgrass in both rooting depth and total root length, but both groups lagged far behind the alien. In the same period, cheatgrass roots reached depths three times greater than Island seedlings and produced 16 times the root length. In sixty days, cheatgrass seedlings produced as much as 190 m of root, and penetrated the soil
column to a depth of 120 cm. In comparison, the greatest root length achieved by
any Idaho fescue seedling was 15.5 m, with a maximum rooting depth of 48 cm.

Island seedlings had 2½ times the root length density of disturbed-site
seedlings, which translates to much better exploitation of soil resources (Caldwell and
Richards 1986; Fitter and Hay 1987). Island seedlings more fully explored the soil
volume in which they were rooted. In a field situation, Island seedlings would have
left less soil outside their depletion zones than would have seedlings from the
disturbed sites. Depletion zone overlap would undoubtedly be much less in disturbed-
site seedlings than in Island seedlings. Because individual tillers within a bunchgrass
are potentially independent (both demographically and functionally) of other tillers in
the grass (Briske 1991), the greater root length density in Island seedlings suggests
greater competition among the roots of neighboring tillers than would occur among
Idaho fescue from the disturbed sites. Island seedlings are likely better competitors
for soil resources than the disturbed-site seedlings.

The root length density of cheatgrass was over six times that of Island
seedlings and over 16 times that of the disturbed-site seedlings. Cheatgrass
intensively explored the soil, producing 6.7 cm of root for every cm³ of soil.
Depletion zone overlap was undoubtedly greater in cheatgrass than in either Idaho
fescue group. Cheatgrass offered greater competition for soil resources than Island or
disturbed-site Idaho fescue.

The disturbed-site seedlings revealed a pattern of root distribution typical of
plants of low fertility or resource poor soils: coarse exploration of a large volume of
soil (Fitter and Hay 1987; Fitter et al. 1988, 1991). Most of this exploration was directed downward rather than laterally. With less than 40% of the root length, disturbed-site seedlings extended roots to nearly 90% of the depth attained by Island seedlings. Island seedlings had 52% of their root biomass in the upper two cm of the soil column. Cheatgrass and the Idaho fescue seedlings from disturbed sites had greater allocation to deeper roots: both had about 42% of their root biomass in the top two cm of soil. Cheatgrass rapidly draws down soil moisture, leaving shallow roots in dry soil (Harris 1967). Differing distributions of root biomass in the two Idaho fescue groups suggest a greater emphasis on moisture uptake in the disturbed-site seedlings. The availability of stored soil moisture increases with depth, especially as the growing season progresses (Larcher 1991; Link et al. 1990; Harris 1967; Richenberger and Pyke 1990), and the availability of mineral nutrients in greatest in the surface horizon (Doescher et al. 1984; Swanson et al. 1986). Positive geotropic growth dominated root extension in seedlings from the disturbed sites, whereas the Island seedlings had much more diageotropic root growth. Root distribution patterns in Idaho fescue populations which have been subjected to 100 years of competition with cheatgrass have changed. The altered root distribution of disturbed-site seedlings likely reflects greater selection for genotypes with deeper root distribution given competition from cheatgrass.

The rate of shoot growth was greater in Island seedlings than in disturbed-site seedlings. Island seedlings produced more and longer leaves. This translated to over three times more leaf area for Island seedlings compared to seedlings from disturbed
sites. Assuming equivalent rates of photosynthesis and water use efficiencies among the two Idaho fescue groups, Island seedlings would have transpired three times more water per unit time. If grown in the same container, Island seedlings would have out-competed seedlings from the disturbed sites for soil moisture as a result of greater leaf area and deeper, more extensive roots. But cheatgrass would out-compete both Idaho fescue groups. Cheatgrass produced more leaves and grew to greater heights, produced more and longer roots, and did it faster, than any Idaho fescue population.

Though Island seedlings grew faster than seedlings from disturbed sites, the two Idaho fescue groups produced biomass with equal efficiency and had similar allocations to root and shoot. Körner (1991) suggested that dry matter partitioning is remarkably constant within a species, and no difference in root weight ratios was found within the two Idaho fescue groups. This similarity allowed the Idaho fescue shoot and root mass observations to be pooled and a single allometric constant calculated for the species. Specific root length and specific leaf area were not different between Island and disturbed-site seedlings. Idaho fescue and cheatgrass produced leaf area with the same efficiency; they had equivalent specific leaf areas. However, Idaho fescue was more efficient than cheatgrass in producing root length, with about 35% more root length per unit biomass. Other than the difference between Idaho fescue and cheatgrass in specific root length, the major differences among the two Idaho fescue groups and the alien were growth rates. Cheatgrass produced biomass much more rapidly than either Idaho fescue group, and Island seedlings grew faster than did seedlings from disturbed sites.
The greater efficiency of Idaho fescue in producing roots may explain why Borman et al. (1991) found Idaho fescue, once established, to successfully compete with alien annuals. If Idaho fescue seedlings managed to survive long enough, they would eventually accumulate sufficient root to effectively compete with cheatgrass. Once an Idaho fescue plant had become established, it would be difficult for cheatgrass to usurp the soil volume occupied by the native. If Idaho fescue populations are maintained primarily through clonal growth (vegetative propagation through fragmentation of large individuals) this could help explain its persistence on invaded rangelands. Such vegets would start their independent existence with a well-developed root system, in contrast to seedlings.

Allocation patterns differed between Idaho fescue and cheatgrass. Idaho fescue invested about \( \frac{1}{8} \) of its carbon in roots, whereas roots accounted for over \( \frac{1}{2} \) of total biomass in cheatgrass. Despite more efficient root production by Idaho fescue, the combination of greater allocation to roots and a higher rate of growth gave cheatgrass a root length:leaf area ratio 1.7 times that of Idaho fescue.

Leaf area and root length have not been reported for Idaho fescue, but Mortimer (1992) and Boot and Mensink (1991) presented data for a closely related species which has the same growth form, sheep fescue. The root weight ratio for sheep fescue was 0.393 (Mortimer 1992); for Idaho fescue, the ratio was 0.286 to 0.326. Boot and Mensink obtained a specific leaf area of 200 cm\(^2\)/g for sheep fescue. Mortimer reported a specific leaf area of 57.7 cm\(^2\)/g and a specific root length of 16,600 cm/g for this species. I obtained values of 245 cm\(^2\)/g and 32,500 cm/g for
these two variables, respectively. Boot and Mensink (1991) reported root length:leaf area ratios of 128 to 175 cm/cm² for sheep fescue, whereas Mortimer reported a ratio of 271 cm/cm². I calculated values of 232 to 267 cm/cm² for Idaho fescue.

Svejcar (1990) measured root length and leaf area in 60 day old cheatgrass seedlings. He reported a root length density of 17 cm/cm³ for the alien, which is 2½ times what I measured. However, Svejcar grew four seedlings in a single (10 x 10 x 10 cm) pot. Harris and Goebel (1976) reported accelerated growth rates in cheatgrass seedlings when grown in competition compared to when grown individually. The combination of neighbors and a differently shaped soil volume may have influenced root growth in Svejcar’s seedlings. Svejcar reported a specific root length of 29,000 cm/g in cheatgrass, which is about a third greater than I found. Our specific leaf area for cheatgrass was 226 cm²/g, and Svejcar reported a maximum of 180 cm²/g after 45 days of growth. By day 60, leaf area had declined in Svejcar’s seedlings because the plants shifted from vegetative to reproductive growth and older leaves were dying.

Our seedlings remained in the vegetative stage throughout the experiment. From data presented by Buman et al. (1988), Svejcar calculated a specific leaf area for cheatgrass of 142 cm²/g, which is as far below Svejcar’s value as our is above.

Svejcar reported a root length:leaf area ratio of 186 cm/cm². The same ratio in our seedlings was 133 cm/cm². I calculated a root weight ratio of 0.55; Svejcar’s seedlings had a root weight ratio of 0.37. Though my methods were often less sophisticated than those used by other researchers, my results compare favorably with theirs.
Plants face a dilemma in growing on western rangelands: they must maximize their capture of photons to realize their greatest growth, but must also produce enough root length to acquire sufficient moisture to sustain CO₂ uptake and photosynthesis. The morphologies of Idaho fescue and cheatgrass reveal two differing strategies for maintaining a favorable water balance. Cheatgrass produces a large amount of resource-capturing surface, both above- and belowground, and has flat, relatively broad leaves. Cheatgrass is an annual, has no drought tolerance, maximizes water uptake during periods when soil moisture is available, and avoids drought as seed (Link et al. 1990). This strategy of low water use efficiency (high rates of uptake and transpiration) is also seen in sagebrush and may be a more successful competitive strategy in semiarid systems (Cohen 1970; DeLucia and Heckathorn 1989; Melgoza et al. 1990; Evans and Black 1993). Idaho fescue is a perennial, produces less leaf and root surface area per unit time than cheatgrass, and has rolled (involute) leaves. Rolled leaves reduce transpiration, by as much as 60 %, by increasing boundary layer resistance and lowering the vapor pressure gradient in the immediate vicinity of stomata (Redman 1985; Larcher 1991). Fine roots more efficiently explore and exploit soil for moisture and nutrients. Idaho fescue survives drought as dormant crowns and roots. Idaho fescue has adaptations that allow greater drought tolerance through water conservation.

A root system that both extends deeply into the soil profile and branches profusely in the upper soil strata allows absorption of water and nutrients during the wet season and extraction of deep, stored moisture during the dry season (Fitter and
Hay 1987). The capacity to absorb water from soil horizons beyond the reach of neighboring species confers a great competitive advantage in seasonally dry environments. Cheatgrass has just this type of root distribution, and enjoys the associated advantage. Cheatgrass root biomass was many times greater than that of Idaho fescue in all horizons, its roots extended to three times the depth, its root density was seven times greater, and it produced twice the root length of the native during the 60 day experiment. Profligate water use and high growth rates likely give a competitive advantage in the semiarid rangeland environment because reduced uptake leaves more available moisture in the soil for neighboring competitors (DeLucia and Heckathorn 1989; Cohen 1970; Evans and Black 1993). Cheatgrass is a much more effective competitor for soil resources than is Idaho fescue. Idaho fescue is better adapted to tolerate the stresses imposed by a semiarid environment, where a lack of moisture delimits the end of the growing season rather than the end of life, as it does for cheatgrass.

Literature Cited


---. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. Ecological Monographs 37:89-111.


CHAPTER VII. COMPETITIVE ABILITY OF SEEDLINGS
FROM
DISTURBED AND UNDISTURBED IDAHO FESCUE POPULATIONS

Jay R. Goodwin, Paul S. Doescher, and Lee E. Eddleman
Introduction

The native perennial bunchgrass, Idaho fescue, is still present on central Oregon rangelands, despite its palatability (Vavra and Sneva 1978; Dragt and Havstad 1987), 125 years of grazing by domestic livestock (Strong 1940; Galbraith and Anderson 1971; Shinn 1977), and invasion by highly competitive alien annuals (Mack 1981). There are at least three plausible explanations for the persistence of Idaho fescue on these grazed and invaded rangelands: the persisting populations are composed of the most competitive genotypes of the original populations; the persisting plants are less palatable genotypes; or they are more tolerant of defoliation. The introduction of domestic livestock and cheatgrass to these rangelands brought new selective pressures to bear on native bunchgrasses (Mack 1981; Mack and Thompson 1982) which could have resulted in ecotypic differentiation. This paper presents the results of a test of the hypothesis that the Idaho fescue populations persisting on grazed and invaded (disturbed) sites have greater competitive ability than a relict population (Driscoll 1964).

If disturbed-site populations of Idaho fescue represent more competitive ecotypes, then plants from these populations should inhibit cheatgrass growth more effectively than plants from a relict population. The more competitive a plant, the greater will be its resource capture, which means reduced resource availability to neighboring plants (Keddy 1989). A reduced availability of resources will reduce plant biomass (Keddy 1989; Spitters 1983). In this experiment, I measured shoot
biomass of Idaho fescue and cheatgrass seedlings from five populations to assess competitive abilities. If the hypothesis were correct, Idaho fescue seedlings from populations persisting on disturbed sites would suppress cheatgrass growth more strongly than seedlings from a relict Idaho fescue population.

Competitive interactions among two species have been investigated using replacement series, wherein total density is held constant while proportions of the two species are varied. However, this method does not account for the effects of varying total density and does not allow differentiation of the effects of inter- and intraspecific competition (Radosevich 1987; Roush et al. 1989; Jolliffe et al. 1984). The addition of monocultures of the competing species at densities greater- and less-than that of the replacement series and more sophisticated methods of analysis correct these shortcomings and quantify the effects of inter- and intraspecific competition (Spitters 1983; Jolliffe et al. 1984).

Materials and Methods

I ran a replacement series experiment, with additional monocultures spanning a range of densities, to assess the competitive abilities of seedlings from disturbed and undisturbed Idaho fescue populations when grown with cheatgrass. In the replacement series, total density (282.5 plants m⁻²) and spatial arrangement (fig. 7.1) were held constant while the density of each species was varied between 0 and 282.5
plants m\(^2\). Monocultures of each species were also planted at densities of 56.5 and 508.5 plants m\(^2\) with spatial arrangement within each density held constant (fig. 7.1).

![Figure 7.1 Spatial patterns for sowing seed at three densities: 56.5, 282.5, and 508.5 plants m\(^2\).](image)

The experiment was run in a greenhouse at Oregon State University, and a randomized, blocked design was used with the blocking factor being greenhouse bench. Diurnal temperatures in the greenhouse alternated between 24 and 18 °C, which are within the range favorable for Idaho fescue and cheatgrass seed germination (Doescher et al. 1985; Young et al. 1981; Young and Evans 1982; Buman and Abernathy 1988). Supplemental lighting was not employed because the investigation was made during summer 1991.

Treatments consisted of five populations of Idaho fescue identified by seed collection site: Combs Flat, Lone Pine, Blanchard, McCoin, and Island. The first four sites have been subjected to long-term grazing by domestic livestock and invasion
by cheatgrass (Strong 1940; Galbraith and Anderson 1971; Shinn 1977); the Island population is taken as representative of an undisturbed site as it has been grazed by domestic livestock only twice (Driscoll 1964) and cheatgrass densities are low (see chapter 2). Cheatgrass seed from the same five sites were also used, and when the two species were grown in mixture, seed from a single location was used. Competitiveness of cheatgrass should not vary among the different cheatgrass populations given the lack of genetic diversity in this species (Novak et al. 1991). Treatments were replicated four times.

Plants were grown in 2832 cm³ pots (15 cm top diameter) filled with soil collected at Combs Flat. Two weeks prior to applying treatments, pots were brought to field capacity using tap water, to allow indigenous seeds to germinate. These representatives of the soil seed bank were removed before treatments were assigned to pots. In the mixtures, each species was randomly assigned to positions, and each complete replacement series plus additional monocultures was randomly assigned to a location within a block. Four seeds were initially planted at each position (fig 7.1), and thinned after emergence to one seedling. Because of differences in germination rates (see chapter 4), cheatgrass seeds were planted five days after Idaho fescue to synchronize emergence of the two species. Pots were again watered to field capacity three days before sowing seeds and were lightly watered following planting. Thereafter, pots were lightly watered (not to field capacity) twice a week by greenhouse staff. Sixty days after planting, shoot material of each seedling was harvested, dried at 50 °C, and weighed.
The introduction of field-collected plant material to the greenhouse by another researcher roughly midway through the experiment resulted in an infestation of aphids. Greenhouse staff applied an insecticidal soap to all plant material in the greenhouse, and sulphur and nicotine were applied on the following day.

Competitive ability was assessed through reciprocal yield analysis, where weighted multiple regression is used to regress the reciprocal of mean biomass per seedling against the densities of conspecifics and competing species (Spitters 1983). The appropriate equations for a two species mixture take the forms of:

\[
\frac{1}{W_1} = \beta_{0,1} + \beta_{1,1}N_1 + \beta_{2,1}N_2
\]

\[
\frac{1}{W_2} = \beta_{0,2} + \beta_{1,2}N_2 + \beta_{2,2}N_1
\]

where \( W \) = dry biomass (g), \( N \) = density (plants m\(^{-2}\)). Subscripts denote \( \beta \)'s 0, 1, and 2, and species 1 and 2. The y-intercept \( (\beta_0) \) is the reciprocal of theoretical maximum biomass of a seedling grown under the conditions of the experiment but without interference, and \( \beta_1 \) and \( \beta_2 \) quantify intra- and inter-specific competition, respectively. The relative competitive ability (RC) of a species is determined by \( \beta_1/\beta_2 \). The product obtained by multiplying RC\(_1\) and RC\(_2\) provides an index for niche differentiation (NDI). An NDI greater than 1 indicates niche differentiation, which means competition between the two species was reduced because they did not each attempt to sequester the same resource at the same time. An NDI less than 1 indicates direct competition for the same iota of resource.

Data from this experiment were fit to Spitters' (1983) model using multiple regression procedures in Number Cruncher Statistical System (Hintze 1990). Weights
were assigned with a robust regression procedure using Andrew’s Sine function (truncation constant = 2.1). The procedure iteratively assigned and adjusted weights until regression coefficients and the absolute value of residuals stabilized. Within each treatment, some observations were assigned a weight of zero (discarded) by this procedure. Once weights had been assigned, weighted multiple regressions were run. Biomass data from both the mixtures and monocultures were used to estimate the regression coefficients, but seedlings which died during the experiment were excluded. Data for the four disturbed-site populations were pooled to test the hypothesis of greater competitive ability in these populations compared to the undisturbed population. Regression equations were also developed for each of the five populations to allow comparison at that level.

Results

The equations developed through reciprocal yield analyses showed shoot growth of cheatgrass seedlings was greatly influenced by intraspecific competition, whereas aboveground production by Idaho fescue seedlings was largely a function of interspecific competition, and cheatgrass seedlings were potentially much larger than Idaho fescue seedlings (table 7.1). Competition from neighboring cheatgrass seedlings had a much greater affect on shoot production by both Idaho fescue and cheatgrass than competition from neighboring Idaho fescue seedlings. Idaho fescue
Table 7.1 Reciprocal yield analysis of shoot production by Idaho fescue and cheatgrass seedlings from disturbed and undisturbed central Oregon sites.

<table>
<thead>
<tr>
<th>Site and Species</th>
<th>Equation $^1$</th>
<th>Adj. $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undisturbed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Idaho fescue</td>
<td>$1/W_F = 2.3268 + 0.0089N_F + 0.22N_C$</td>
<td>0.87</td>
</tr>
<tr>
<td>cheatgrass</td>
<td>$1/W_C = -0.0519 + 0.007N_C + 0.0005N_F$</td>
<td>0.87</td>
</tr>
</tbody>
</table>

| Disturbed        |              |            |
| Idaho fescue     | $1/W_F = 7.638 + 0.0027N_F + 0.3547N_C$ | 0.85 |
| cheatgrass       | $1/W_C = 0.0106 + 0.0064N_C + 0.00006N_F$ | 0.86 |

1. Subscripts identify Idaho fescue (F) and cheatgrass (C).

Seedlings from the undisturbed site were better competitors than Idaho fescue seedlings from the disturbed-site populations.

The equations for seedlings from the undisturbed site were both highly significant (Idaho fescue: $F=267.68$, $p<0.000$; cheatgrass: $F=313.11$, $p<0.000$). However, the regression coefficient for Idaho fescue density (a measure of interspecific competition) was not significantly different from zero in the equation describing reciprocal yield of cheatgrass ($t=0.63$, $p=0.528$). With cheatgrass density as the only independent variable, the model had an $R^2$ of 0.8738; adding Idaho fescue density did not change $R^2$ (0.8743).

These equations reveal great differences between Idaho fescue and cheatgrass. An Island Idaho fescue seedling grown under the conditions of this experiment and without interference was theoretically capable of producing 0.43 g of dry shoot biomass, whereas a great deal more would be produced by a cheatgrass seedling under the same conditions. Experimental error prevented a precise estimate of $\beta_0$ for
cheatgrass (standard error of the estimate was 0.1499), but the potential maximum shoot biomass of the alien annual was clearly much greater than that of Idaho fescue. Using the upper limit of the 95% confidence interval of $\beta_0$ to estimate the 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. A value closer to the midpoint of the interval gives a higher prediction (e.g. using 0.01 predicts 100 g of biomass).

The RC of Island Idaho fescue was 0.0407. An Idaho fescue seedling had only 0.04 times the effect on a neighboring Idaho fescue as did a neighboring cheatgrass seedling; 25 Idaho fescue seedlings were required to provide the same intensity of interference as did a single cheatgrass seedling (Fig. 7.2). The RC of cheatgrass was 13.0966. This means a single cheatgrass seedling interfered with resource capture and growth by a neighboring cheatgrass seedling as much as did 13 Island Idaho fescue seedlings (Fig. 7.2). Multiplying the RC's of the two species gave an NDI of 0.53, indicating intense, direct competition between seedlings of the two species. Of the two species, cheatgrass was clearly the superior competitor, as shown by the coefficients for inter- and intraspecific competition in the two equations.

Both models were also highly significant (Idaho fescue: $F=927.0$, $p<0.000$; cheatgrass: $F=1092.66$, $p<0.000$) for the disturbed site seedlings. In both equations, however, the regression coefficient for Idaho fescue density was not significantly different from zero (Idaho fescue: $t=0.83$, $p=0.406$; cheatgrass: $t=0.14$, $p=0.889$).
Figure 7.2 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the undisturbed site given intra- and interspecific competition. The steeper the slope of the plane, the greater the independent variable’s influence.
As with seedlings from the undisturbed site, there was a tremendous difference in maximum potential shoot biomass of the two species. In the absence of interference, a cheatgrass seedling from the disturbed sites was predicted to produce as much as 94.4 g of dry shoot biomass. In comparison, the shoot of an Idaho fescue seedling from the same sites and grown under the same conditions had a theoretical maximum dry weight of 0.13 g.

The RC of disturbed-site Idaho fescue was 0.0077. The presence of a conspecific neighbor interfered with the growth of an Idaho fescue seedling only 0.008 times as much as did a neighboring cheatgrass seedling (Fig. 7.3). A disturbed-site Idaho fescue seedling would have had to be surrounded by 131 conspecifics to have its resource capture and growth inhibited to the same extent as was caused by a single cheatgrass seedling. The RC of cheatgrass from the disturbed sites was 112.26. The presence of a single cheatgrass neighbor had the same influence on the growth of a cheatgrass seedling as did the presence of 112 Idaho fescue seedlings. Idaho fescue offered only 0.009 times the interference of cheatgrass (Fig. 7.3). The NDI for the two disturbed-site species was 0.86; the species directly competed for resources when grown in mixture.

Analysis of the data at the level of individual populations gave the results: cheatgrass was the superior competitor and caused the greatest interference to the growth of seedlings of both species, and Idaho fescue seedlings from the undisturbed Island population were better competitors than were conspecifics from the other populations (table 7.2). The models for shoot production by Combs Flat seedlings
Figure 7.3 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the disturbed sites given intra- and interspecific competition. Both species were most influenced by cheatgrass. Idaho fescue had no affect on cheatgrass growth.
Table 7.2 Reciprocal yield analysis of shoot production by Idaho fescue and cheatgrass seedlings from ten populations at five central Oregon sites.

<table>
<thead>
<tr>
<th>Site and Species</th>
<th>Equation¹</th>
<th>Adj. R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>1/Wₚ = 2.3268 + 0.0089Nₚ + 0.22Nₜ</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>1/Wₜ = -0.0519 + 0.007Nₜ + 0.0005Nₚ</td>
<td>0.87</td>
</tr>
<tr>
<td>Combs Flat</td>
<td>1/Wₚ = 11.8234 + 0.0035Nₚ + 0.57Nₜ</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>1/Wₜ = 0.1151 + 0.0059Nₜ + 0.0001Nₚ</td>
<td>0.84</td>
</tr>
<tr>
<td>Lone Pine</td>
<td>1/Wₚ = 4.4238 + 0.0087Nₚ + 0.2407Nₜ</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>1/Wₜ = -0.1596 + 0.007Nₜ + 0.0002Nₚ</td>
<td>0.87</td>
</tr>
<tr>
<td>Blanchard</td>
<td>1/Wₚ = 5.1823 + 0.0065Nₚ + 0.3103Nₜ</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>1/Wₜ = 0.0898 + 0.0059Nₜ + 5x10⁻⁶Nₚ</td>
<td>0.86</td>
</tr>
<tr>
<td>Mc Coin</td>
<td>1/Wₚ = 4.836 + 0.0019Nₚ + 0.3321Nₜ</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>1/Wₜ = -0.1652 + 0.0077Nₜ + 0.0004Nₚ</td>
<td>0.89</td>
</tr>
</tbody>
</table>

1. Subscripts identify Idaho fescue (F) and cheatgrass (C).

were both statistically significant (Idaho fescue: F=347.45, p<0.000; cheatgrass: F=237.79, p<0.000), but the coefficients for Idaho fescue density were not significantly different from zero (Idaho fescue: t=0.38, p=0.709; cheatgrass: t=-0.14, p=0.889). A cheatgrass seedling from this population grown without interference was predicted to produce 100 times (8.69 g) the dry shoot biomass of a Combs Flat Idaho fescue seedling (0.08 g).

The RC of Combs Flat Idaho fescue was 0.0061: an Idaho fescue seedling from this population gave only 0.006 as much interference to a neighboring conspecific as did a cheatgrass seedling (Fig. 7.4). A single cheatgrass seedling had the same influence on an Idaho fescue seedling as did 165 neighboring Idaho fescue
Combs Flat

Figure 7.4 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the Combs Flat site given intra- and interspecific competition. For both species, competition from cheatgrass greatly affected production.
seedlings. Cheatgrass had an RC of 59. A cheatgrass seedling with a single conspecific neighbor experienced the same interference as it would had it been surrounded by 59 Idaho fescue seedlings. That is, a single Combs Flat Idaho fescue seedling offered only 0.017 times the competition to a cheatgrass seedling as did a neighboring conspecific seedling (Fig. 7.4). The NDI for the two Combs Flat species was 0.36; cheatgrass and Idaho fescue competed directly when grown in mixture.

Both Lone Pine equations were statistically significant (Idaho fescue: $F=247.60, p<0.000$; cheatgrass: $F=308.89, p<0.000$). In the equation for cheatgrass yield, the coefficient for Idaho fescue density was not significantly different from zero ($t=0.24, p=0.814$). The same coefficient just failed the significance test ($t=1.84, p=0.069$) in the model describing the Idaho fescue response, and the 95% confidence interval for the estimate included zero. Again, cheatgrass was predicted to produce much more shoot biomass than Idaho fescue when grown without interference, though experimental error prevented a precise estimate of the y-intercept (standard error of the estimate was 0.153). The minimum predicted dry shoot biomass for Lone Pine cheatgrass was 6.92 g based on the 95% confidence interval for $\beta_0$.

Idaho fescue from the Lone Pine population had an RC of 0.0362, meaning that an Idaho fescue seedling surrounded by 28 conspecific seedlings experienced the same interference as it would given a single cheatgrass neighbor (Fig. 7.5). The RC of cheatgrass from this site was 33.1. The responses of a cheatgrass seedling with a single conspecific neighbor and that of a cheatgrass seedling influenced by 33 Idaho
Figure 7.5 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the Lone Pine site given intra- and interspecific competition. Competition from Idaho fescue had little influence on the growth of both species.
fescue seedlings were predicted to be the same (Fig. 7.5). The NDI for Lone Pine Idaho fescue and cheatgrass grown in mixture was 1.12, suggesting niche differentiation and a lessening of direct competition between the two species.

For seedlings of the Blanchard populations, both equations were statistically significant (Idaho fescue: \( F=275.04, p<0.000 \); cheatgrass: \( F=289.74, p<0.000 \)). Again, however, the coefficient for the density of Idaho fescue was not significantly different from zero in either (Idaho fescue: \( t=1.42, p=0.161 \); cheatgrass: \( t=0, p=1 \)). The potential maximum dry shoot biomass of cheatgrass (11.14 g) was predicted to be much greater than that of Idaho fescue (0.19 g) when grown without interference under the conditions of the experiment.

Idaho fescue seedlings of the Blanchard population had a RC of 0.0209. To experience the same interference as it would given a single cheatgrass neighbor, an Idaho fescue seedling would need to be surrounded by 48 conspecifics (Fig. 7.6). The RC of cheatgrass was 11,800. Blanchard cheatgrass was insensitive to the presence of Idaho fescue seedlings from the Blanchard population (Fig. 7.6). An incredible 11,800 Idaho fescue seedlings were predicted to elicit the same response in a cheatgrass seedling as would a single neighboring conspecific; Blanchard Idaho fescue did not inhibit cheatgrass growth. The NDI for the Blanchard species was 246.62. Competition between the two species was essentially eliminated by niche differentiation; the two species did not attempt to capture the same iota of resource.

Both equations for the McCoin seedlings were statistically significant (Idaho fescue: \( F=498.39, p<0.000 \); cheatgrass: \( F=344.99, p<0.000 \)), though the
Figure 7.6 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the Blanchard site given intra- and interspecific competition. Competition from Idaho fescue had essentially no influence on either species.
coefficient for Idaho fescue density was not significantly different from zero in either (Idaho fescue: t=0.4, p=0.692; cheatgrass: t=0.46, p=0.647). Experimental error again precluded a precise estimate of the reciprocal of maximum potential dry shoot biomass of cheatgrass (standard error of the estimate was 0.142), but it is clear that cheatgrass is predicted to produce far more than the 0.21 g predicted for McCoin Idaho fescue. Cheatgrass from this site was predicted to produce a minimum of 8.54 g of dry shoot biomass, using the 95% confidence interval of $\beta_0$.

The RC of McCoin Idaho fescue was 0.0056. One hundred and seventy-nine Idaho fescue seedlings were predicted to have the same influence on growth of an Idaho fescue seedling as had by a single cheatgrass neighbor (Fig. 7.7). Cheatgrass from the McCoin site had an RC of 20.63, meaning that a cheatgrass seedling responded similarly to a single conspecific neighbor or to 21 adjacent Idaho fescue seedlings (Fig. 7.7). In mixture, the two species had an NDI of 0.12. There was no niche differentiation and the two species competed directly with one another.

Discussion

This experiment tested the hypothesis of greater competitive ability in Idaho fescue populations which have persisted on disturbed rangelands despite the presence of highly competitive alien annuals. The results do not support the hypothesis. Using the competitive influence of a single cheatgrass seedling as a basis for comparison, it took fewer (13) seedlings from the undisturbed population of Idaho fescue, versus the
Figure 7.7 Regression planes for reciprocal yield of cheatgrass (A) and Idaho fescue (B) from the McCoin site given intra- and interspecific competition. Both species were most affected by competition from cheatgrass.
disturbed-site populations (112), to exert the same competitive pressure on a neighboring cheatgrass seedling. Though this comparison equates the competitive ability of different cheatgrass populations, it is likely valid because of the extreme lack of genetic diversity in cheatgrass throughout its North American range (Novak et al. 1991). Among Idaho fescue seedlings, interspecific competition was always more influential on their growth than was intraspecific competition. Interspecific competition from Idaho fescue had little effect on the growth of cheatgrass seedlings, while intraspecific competition had great influence.

If improved competitive ability were the reason behind persistence of Idaho fescue on cheatgrass-invaded rangelands, then cheatgrass growth should have been less when grown with disturbed-site Idaho fescue than when grown with Idaho fescue from the undisturbed site as a neighbor. That is, disturbed-site Idaho fescue should have interfered with cheatgrass growth more than Idaho fescue from the undisturbed Island site. I found Idaho fescue from the undisturbed site to be more of a competitor to cheatgrass than were seedlings from the disturbed-site populations. Thirteen seedlings from the Island population of Idaho fescue provided the same intensity of interference to a growing cheatgrass seedling as did a single conspecific neighbor. Taken as a whole, disturbed-site Idaho fescue was much less competitive, with 112 seedlings required to equal a single cheatgrass seedling. When considered individually, all four of the disturbed-site Idaho fescue populations were less effective competitors than was the Island population. The number of Idaho fescue seedlings required to provide the same intensity of interference to a cheatgrass seedling as a
neighboring conspecific was 21, 33, 59, and 11,800 for the McCoin, Lone Pine, Combs Flat, and Blanchard populations, respectively. The number of Blanchard seedlings required to equal a single cheatgrass seedling should not be interpreted literally; rather, it shows that Blanchard Idaho fescue had no effect on the growth of cheatgrass. Clearly, Island Idaho fescue had a greater competitive influence on cheatgrass than did any of the disturbed-site populations.

The number of Idaho fescue seedlings required to provide the same intensity of competition to an Idaho fescue seedling as cheatgrass also shows seedlings from the Island population to be better competitors. The number of Idaho fescue seedlings required to equal cheatgrass was 25, 28, 48, 165, and 179 for the Island, Lone Pine, Blanchard, Combs Flat, and McCoin populations, respectively. Considering the disturbed site populations together, 131 Idaho fescue seedlings gave the same intensity of interference to an Idaho fescue seedling as a single neighboring cheatgrass seedling.

Examination of the regression coefficients which quantify the effects of inter- and intraspecific competition shows cheatgrass to be the superior competitor of the two species, and also supports the argument of greater competitive ability in the Island population of Idaho fescue. The coefficient for interspecific competition for cheatgrass growth was greatest when cheatgrass was grown with Idaho fescue from the Island, describing greater interference caused by this population compared to the other Idaho fescue populations. However, the coefficients for intraspecific competition in the equations describing the response of cheatgrass were always much
greater than were the coefficients for interspecific competition. In fact, \( \beta_2 \) was not significantly different from zero in all the equations describing cheatgrass yield; Idaho fescue did not have a statistically significant competitive effect on cheatgrass growth.

In the case of an Idaho fescue seedling, cheatgrass always had great competitive influence, but only in the case of the Island population did conspecifics have a significant competitive effect as well. (Intraspecific competition \( p=0.069 \) barely failed the significance test \( \alpha=0.05 \) in the Lone Pine population of Idaho fescue.)

The persistence of Idaho fescue on sites invaded by cheatgrass and grazed by domestic livestock is not due to greater competitive abilities. Idaho fescue populations from these disturbed sites were actually less effective competitors than was the Island population. This finding supports the results of the root growth experiment described in chapter 6. Resource capture, and hence competitive success, is a function of the growth and positioning of resource-absorbing organs (Grime 1979; Fitter and Hay 1987). Island seedlings had the greater root and shoot biomass, root length density, leaf area and shoot height, and extended roots to greater depth than did Idaho fescue seedlings from the disturbed sites. In the replacement series, Idaho fescue seedlings from the undisturbed site were predicted to produce as much as 0.43 g of dry shoot biomass if grown without interference, whereas only 0.13 g was predicted for conspecifics from the disturbed sites. In comparison, cheatgrass seedlings were predicted to produce as much as 94.4 g of dry shoot biomass. Though this is certainly a huge quantity of biomass for an annual to produce in a single
season, it is possible given the tremendous environmentally-controlled phenotypic plasticity of cheatgrass.

Seedling survival on western rangelands depends upon effective competition for limited moisture stored in the soil profile during winter (Harris 1967; Reichenberger and Pyke 1990; Melgoza et al 1990; Eissenstat and Caldwell 1988). In this experiment, I attempted to water the pots frequently enough to prevent mortality but not so frequently as to prevent periodic water stress. I did have seedlings die, probably due to interference from neighbors, and near the end of the experiment, cheatgrass seedlings lost turgor before the next watering. In most cases, cheatgrass and Idaho fescue directly competed for growth-sustaining resources, as shown by NDI’s. In the cases of Blanchard and Lone Pine Idaho fescue, niche differentiation occurred. Blanchard Idaho fescue, in particular, did not impair resource capture by cheatgrass. This lack of an interaction is probably due to differences in growth rates. Of the five Idaho fescue populations, Blanchard and Lone Pine had the lowest rates of root growth at the end of 56 days, and cheatgrass growth was far more rapid than any Idaho fescue population (see chapter 6). The Blanchard and Lone Pine seedlings may never have attained sufficient size to affect cheatgrass growth.

I believe the competition between Idaho fescue and cheatgrass was primarily for soil resources, though competition for light likely played a role late in the experiment when many Idaho fescue leaves were overtopped by a cheatgrass canopy. The growth responses of Island Idaho fescue described in the root growth experiment (chapter 6) reveal the morphological traits that confer greater competitive ability to
this population relative to those from the disturbed sites. The greater root length
density, rooting depth, leaf area, and shoot height of Island seedlings allows greater
resource capture and competitive success.

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CHAPTER VIII. SUMMARY, CONCLUSIONS, AND OTHER THOUGHTS
But by far the most important consideration is that the chief part of the organization of every being is simply due to inheritance

Charles Darwin (1859)

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 evolutionary change in a population (if any) is constrained within the limits of its genetics.

Summary and Conclusions

The experiments described in this thesis sought to determine whether greater competitive ability explained the persistence of Idaho fescue on central Oregon rangelands that have been subject to long-term grazing by domestic livestock and invasion by highly competitive alien plant species. Comparisons were made between five Idaho fescue populations, four from grazed and invaded (disturbed) sites and one from a relict (undisturbed) area, to determine which group or population had the greater competitive ability. Our criteria for assessing competitiveness varied with experiment, but were based on accepted ecological principles in all studies, and we used a very competitive co-occurring alien species, cheatgrass, as a yardstick against which to measure competitive ability in Idaho fescue.

Plant growth in central Oregon is dependent upon soil moisture accumulated during winter, because summers are typically droughty. The root phenology of cheatgrass allows the alien to withdraw soil moisture from the soil profile prior to the exploration of the same soil volume by roots of native seedlings. Seedlings that emerge subsequent to cheatgrass are effectively denied soil moisture, and desiccate and die. Cheatgrass, being an annual, must rely on seed to re-establish its populations. Idaho fescue, being a perennial which reproduces by seed and tillers, relies on seed for recruitment, though the perennial is afforded many more opportunities over the course of its life for seed production, dispersal, and
establishment. Though seedlings likely play a small role in year to year population maintenance, seedlings offer the potential for adaptation and evolutionary change.

In our investigation of the germination of Idaho fescue seed, we viewed the speed of germination as an indicator of potential success in the competition for space, as early emergence is well correlated with space capture, growth, and survival (Ross and Harper 1972; Weiner 1985; Harris 1967). We also studied the inhibitory effect of increasing water stress on germination, reasoning that better competitors would be less sensitive to this stress. Because cheatgrass germinates in the fall, and puts down roots during the winter, we used temperature and light regimes that simulated fall in central Oregon. Seeds from the undisturbed Idaho fescue population began germinating sooner and achieved a greater rate and percentage of germination than did the undisturbed group over all temperature + light regimes and all levels of water stress. However, increasing water stress slowed Idaho fescue germination. Cheatgrass seed germination was much less sensitive to increasing water stress, and was much more rapid, than Idaho fescue. Rapid germination, early emergence, and swift space capture do not explain the persistence of Idaho fescue on the disturbed sites. The Idaho fescue population from the undisturbed site had the greater competitive ability in this regard. However, neither of the two Idaho fescue groups showed the potential to offer cheatgrass serious competition during the establishment phase.

We investigated after-ripening requirements in Idaho fescue, because they had not been previously investigated and because germination will not occur until any
such requirement has been satisfied. The germinability of Idaho fescue seed increases to a maximum during the first six months following seed shatter. That is, the potential for germination in a pool of Idaho fescue seeds is greatest in the early spring following seed shatter. This is also the time when soil moisture is most likely to favor establishment and survival. In comparison, 50% of the cheatgrass seed crop is germinable at shatter, and after-ripening requirements are satisfied within two weeks (Thill et al. 1979; Young et al. 1969). In general, a cheatgrass population enjoys a six month head start over a competing population of Idaho fescue seedlings in the race for space.

Because resource uptake and hence competitive success is a function of the amount, activity, and distribution of resource-absorbing plant organs (Grime 1979; Fitter and Hay 1987; Larcher 1991), we studied the morphology and growth of Idaho fescue and cheatgrass seedlings when grown without interference. Seedlings from the undisturbed Idaho fescue population emerged sooner, had greater root length density, leaf area, shoot height, and rooting depth than did conspecific seedlings from the disturbed sites. However, seedlings of both groups were equally efficient in producing roots and leaves on a per unit biomass basis: specific leaf area and specific root length were the same for all the Idaho fescue populations. As in the germination experiment, cheatgrass showed attributes suggesting far greater competitive ability than Idaho fescue. Cheatgrass seedlings emerged considerably earlier than Idaho fescue seedlings, and had much greater root length density, leaf area, shoot height, and rooting depth. Specific leaf area of cheatgrass was equal to that of Idaho fescue,
but the native bunchgrass had a higher specific root length than the alien. The results of this experiment suggest that cheatgrass would be far more successful in capturing both soil and light resources in a competition with Idaho fescue seedlings. Once established, it would be difficult for cheatgrass to displace Idaho fescue, but in a competition among seedlings for establishment and survival, cheatgrass would easily win.

Interestingly, root growth patterns differed between the disturbed and undisturbed Idaho fescue. The majority of root biomass for Idaho fescue from the undisturbed site was in the upper 2 cm of the soil profile, whereas the seedlings from disturbed sites had less than half of their root biomass in the same strata. Though the seedlings from the disturbed sites averaged only 40% of the root length produced by undisturbed-site Idaho fescue, they extended roots to 90% of the depth reached by the faster growing seedlings from the undisturbed site. Roots of seedlings from the disturbed sites showed a stronger tendency for growth down the soil column than did those from the undisturbed population.

The competitive abilities of the five Idaho fescue populations were assessed using a replacement series experiment, where the native was grown in mixture with cheatgrass. Weighted multiple regression (Spitters 1983) was used to measure the influence of density on seedling shoot biomass for both Idaho fescue and cheatgrass. The results of the replacement series support the findings of the earlier experiments. Cheatgrass shoot biomass was much greater than that of Idaho fescue, and cheatgrass growth was essentially insensitive to the density of neighboring Idaho fescue.
Intraspecific competition explained virtually all of the variation in cheatgrass shoot biomass. Though all five of the Idaho fescue populations had very little effect on cheatgrass growth, seedlings of the undisturbed Idaho fescue population had the greatest influence. Cheatgrass growth was often enhanced by greater densities of Idaho fescue, though not because of any parasitic or symbiotic interaction. Because an increase in Idaho fescue density meant a decrease in cheatgrass density in the replacement series (where total density was held constant), a greater density of Idaho fescue resulted in a lessening of intraspecific competition. For Idaho fescue, interspecific competition largely controlled shoot biomass. Only in the undisturbed population was intraspecific competition a statistically significant factor. Of the two species, cheatgrass is the far better competitor, and of the five Idaho fescue populations, the undisturbed population is the most competitive.

The results of these investigations have produced a clear answer to our question: the persistence of Idaho fescue on degraded central Oregon rangelands is not due to greater competitive ability in the enduring populations. The Idaho fescue population from the undisturbed site showed greater competitive ability than the populations from disturbed sites. But, importantly, even seedlings from the undisturbed Idaho fescue population did not offer effective competition to cheatgrass; Idaho fescue seedlings did not interfere with cheatgrass growth to a significant degree.
Some Additional Thoughts

If competitive success does not explain the persistence of the Idaho fescue populations on disturbed sites, what could? Two other possibilities have already been mentioned: reduced palatability and increased tolerance for defoliation. I cannot reject these possibilities as I have not tested them, but personal observations suggest the first hypothesis is unlikely to be true: on the disturbed sites where grazing is occurring presently, livestock make good, often heavy, use of Idaho fescue (e.g. Lone Pine, McCoin Orchard). I cannot say anything regarding differences in grazing tolerance, as I have neither data nor observations for the response to defoliation of the disturbed and undisturbed populations. I can say, however, that defoliation removes photosynthetic tissue thereby reducing the carbon available for biomass production, and that regrowth is dependent upon current photosynthates rather than stored carbohydrates (Caldwell et al. 1981; Richards and Caldwell 1985; Belsky 1986; Briske 1991). I know also that reduced growth means at least a reduction in the rate of resource capture, if not a loss of previously occupied space (sensu Ross and Harper 1972). Hence, it logically follows that even with increased tolerance for defoliation, Idaho fescue population size and recruitment are likely to be reduced by grazing (Briske 1991; Belsky 1992). If cheatgrass is not grazed, as is often the case (because of the short period during which it is attractive to the grazer, and because good management often precludes the introduction of livestock to the site until after seed shatter in Idaho fescue, by which time cheatgrass has died and dried), the competitive
ability of Idaho fescue relative to cheatgrass can only be diminished (Briske 1991). The theory of herbivore-optimization of grass growth (McNaughton 1979) is fallacious (Belsky et al. 1993).

It would appear then, that an explanation for the persistence of Idaho fescue populations on grazed and invaded sites remains to be developed. There are, undoubtedly, many factors contributing to this persistence, including stochastic elements in livestock grazing and forage selection and physical impediments to livestock movement. But these two factors are, I believe, relatively inconsequential. Rather, as the original research hypothesis upon which this study was predicated held, I believe there is a fundamental genetic basis for the persistence of Idaho fescue on these grazed and invaded central Oregon rangelands. I now present an argument to explain this persistence that has its roots in the two quotations that opened this chapter, and I will use Grime’s (1977, 1979) theory of the evolution of plant strategies to frame the argument.

Grime (1977, 1979) argues that three primary strategies for plant survival of disturbance and stress have evolved (Table 8.1). In Grime’s theory, the selection pressures inherent to an environment drive the indigenous plant species toward a particular, genetically-based strategy, or suite of traits, that confer fitness. Given differing environments and thus differing selection pressures, different adaptations are selected for and become fixed in the population. Some of the traits which typify the three strategies posited by Grime are presented in Table 8.2. It is important to note that each strategy represents a pole on a continuum (Fig. 8.1), and that most plants
Table 8.1 The roles of disturbance and stress in the evolution of plant strategies according to Grime (1979).

<table>
<thead>
<tr>
<th>Intensity of Disturbance</th>
<th>Intensity of Stress</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
</tr>
<tr>
<td>Low</td>
<td>Competitive Strategy</td>
</tr>
<tr>
<td>High</td>
<td>Ruderal Strategy</td>
</tr>
</tbody>
</table>

1. Disturbance is defined as the processes which limit plant biomass through physical destruction of plant tissue (e.g. herbivory, fire). 2. Stress is defined as the environmental constraints that limit the rate of primary production (e.g. drought, nutrient deficiency).

Figure 8.1 Grime’s (1979) model of plant strategies. The position of a species shows the relative influences of competition, stress tolerance, and recovery from biomass-destroying disturbance in the species’ evolution of a strategy for survival.
Table 8.2 Traits associated with the competitive, stress-tolerant, and ruderal strategies posited by Grime (1979).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Competitive</th>
<th>Stress-tolerant</th>
<th>Ruderal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life form</td>
<td>herbs, shrubs, trees lichens, herbs, shrubs, trees</td>
<td>lichens, herbs, shrubs, trees</td>
<td>herbs</td>
</tr>
<tr>
<td>Plant longevity</td>
<td>long or rather short long to very long</td>
<td>very short</td>
<td>short</td>
</tr>
<tr>
<td>Shoot morphology</td>
<td>high, dense canopy many forms</td>
<td>small, narrow canopy</td>
<td></td>
</tr>
<tr>
<td>Leaf form</td>
<td>mesomorphic</td>
<td>coriaceous, acicular mesomorphic</td>
<td></td>
</tr>
<tr>
<td>Leaf longevity</td>
<td>rather short</td>
<td>long</td>
<td>short</td>
</tr>
<tr>
<td>Leaf phenology</td>
<td>peak production during favorable period(s)</td>
<td>evergreens, various phenologies</td>
<td>brief peak production during favorable period</td>
</tr>
<tr>
<td>Phenology of flowering</td>
<td>usually after periods of maximum potential productivity</td>
<td>no relationship between season and flowering</td>
<td>early in life-history</td>
</tr>
<tr>
<td>Frequency of flowering</td>
<td>usually every year intermittent over long life-history</td>
<td>annually or more often</td>
<td></td>
</tr>
<tr>
<td>Allocation to seeds</td>
<td>small</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Perennation</td>
<td>buds, seeds</td>
<td>leaves, roots</td>
<td>seeds</td>
</tr>
<tr>
<td>Maximum potential growth rate</td>
<td>rapid</td>
<td>slow</td>
<td>rapid</td>
</tr>
<tr>
<td>Response to stress</td>
<td>allocation to vegetative growth</td>
<td>little change in allocation patterns</td>
<td>allocation to flowering</td>
</tr>
<tr>
<td>Photosynthesis and nutrient uptake</td>
<td>seasonal, coincides with growth</td>
<td>opportunistic, often uncoupled from growth</td>
<td>opportunistic, coincides with growth</td>
</tr>
<tr>
<td>Physiological acclimation</td>
<td>weakly developed</td>
<td>strongly developed</td>
<td>weakly developed</td>
</tr>
<tr>
<td>Carbohydrate storage</td>
<td>little storage</td>
<td>leaves, stems, or roots</td>
<td>seeds only</td>
</tr>
<tr>
<td>Litter</td>
<td>copious, often persistent</td>
<td>sparse, sometimes persistent</td>
<td>sparse, usually transient</td>
</tr>
</tbody>
</table>
actually lie somewhere on the three dimensional continuum bound by the three strategies. That is, most plants are stress-tolerant competitors, or competitive ruderal, or some other intergradation rather than purely a competitor, ruderal, or stress tolerator.

The selection pressures imposed by a population's environment are fundamental to Grime's theory. The environment of central Oregon was described in Chapter 2. Weather is highly variable and unpredictable beyond a general statement of winter being wet and summer being dry (Anon. 1983, 1981-1989). Freezing temperatures are possible in any month of the year, diurnal temperature fluctuations are very great, and the probability of drought is high. The growing season is typified by summer drought, which results in the death of annuls and dormancy in most perennials, particularly herbaceous species. Plant growth in these environments may be limited by the availability of nitrogen as well (Smith and Nowak 1990). The rate at which biomass can be produced by a plant in this environment is constrained by the fluctuating availability of resources: the rangeland environment imposes stress upon rangeland plants. These stresses are a property of the environment, not simply the result of interference from competing species, though stress can certainly be aggravated by interference (Harris 1967; Grime 1979; Melgoza et al. 1990). Prehistorically, disturbance has played a lesser role to stress in this system. Periodic fires did occur, as often as every five years at some sites but with a fire-return interval averaging 10-50 years (Burkhardt and Tisdale 1976; Wright et al. 1979; Martin 1982). Additionally, these fires were most likely during the hot months of
summer, when thunderstorms provided the spark and dry, dormant grasses the fuel. Damage to grasses at this time would have been minimized because of growth form and dormancy. Disturbance by grazing ungulates was minimal as well, particularly compared to the Great Plains, simply because the habitat did not support large herds (Mack and Thompson 1982). The relative sparseness of watering holes and a lack of good feed for lactating females kept ungulate populations small.

The rangeland environment prior to settlement was characterized by a high intensity of stress and a low intensity of disturbance. The rangeland grasses native to central Oregon evolved under these general conditions, and these selection pressures would drive a population toward Grime’s stress-tolerant strategy. In his book, Grime (1979:67) states, “Stress tolerant competitors are strongly represented among the grasses and sedges exploiting the semi-arid conditions of the North American prairies and the Russian Steppes.”

If we consider Grime’s theory, making specific consideration of Idaho fescue and cheatgrass, we can say the following things. Cheatgrass has a very short (<1 year) life span, allocates a great deal of its carbon to seed production, is capable of very rapid growth and morphological changes, produces most of its aboveground organs during a brief period in the spring when conditions are most favorable, avoids drought stress by shifting allocation to seed production followed shortly by senescence and death, and relies entirely upon seeds for regeneration. In short, cheatgrass has the attributes of a competitive ruderal; it lacks the attributes of a stress tolerant species. Idaho fescue, on the other hand, is a stress tolerant competitor. Idaho
fescue is a perennial species, allocates relatively little of its annual production to seeds (especially during periods of stress, e.g. drought), has an inherently slow growth rate, avoids drought stress as both dormant buds and seeds, relies on both vegetative expansion and seeds for regeneration, and produces most of its aboveground organs when environmental conditions (primarily moisture availability) are most favorable. Though it has not been investigated in Idaho fescue, the capacity for rapid morphological adjustment in response to environmental changes (e.g. nutrient rich microsites) has been studied in bluebunch wheatgrass, another common, native bunchgrass which co-occurs with Idaho fescue and evolved in the same system. Bluebunch wheatgrass showed no morphological response to nutrient-rich soil microsites, though Eurasian congeners did (Jackson and Caldwell 1989). Cheatgrass lies far towards the ruderal pole while Idaho fescue falls in the region of stress-tolerant competitors. The major differences between the two species are rapid growth and morphological adjustment in cheatgrass, which gives great competitive ability, and slow, largely invariable growth rates and morphology in Idaho fescue, which makes for poor competitiveness, particularly as a seedling (Fitter and Hay 1987).

In view of the pressures which have directed Idaho fescue evolution and the suite of traits the species possesses, I suggest that the persistence of Idaho fescue on degraded central Oregon rangelands is due to greater stress tolerance rather than greater competitiveness. Because of archetype effects, there are limits to the range of genetically-based adaptations that can occur in a population (Harper 1982). Where natural selection has driven a species’ evolution towards a genotype that is stress
tolerant, rather than one that emphasizes rapid resource capture and competitiveness, ecotypic variation that gives greater stress tolerance is more probable than is a major new direction in the genetics of a population. For a plant having a stress tolerant genotype, the interference caused by competitive aliens probably elicits the same response as would greater environmental stress (such as drought).

I suggest that because of new selective pressures, due to introductions domestic livestock and alien plants, ecotypic differentiation has occurred in Idaho fescue populations of disturbed and undisturbed sites, with the populations of disturbed sites having greater stress tolerance. Invasion by cheatgrass did not result in selection for more competitive genotypes in Idaho fescue, because the gene pool in Idaho fescue lacks the genetic information that could give the ability to compete successfully with cheatgrass. But that gene pool did include alleles that allow Idaho fescue to survive prolonged drought, and it is primarily by withdrawing soil moisture that cheatgrass affects native bunchgrasses. The traits noted in these studies support the theory of more stress tolerant genotypes in the Idaho fescue populations from disturbed sites, most particularly the inherently slow growth rates and smaller size compared to the population from the undisturbed site. Fitter and Hay (1987) noted that the physiology and morphology of plants indigenous to infertile soil are less flexible than those of plants from fertile sites; they are usually “slow-growing and tend not to respond morphologically to changes in nutrient [resource] concentration.” These traits, among others, enable efficient soil exploration and resource uptake in infertile soil (Fitter and Hay 1987), and are typical of stress-tolerant plants.
Additional support for this theory was presented by Nasri (1993). He grew Idaho fescue (from the same sites as in this study) in mixture with cheatgrass using an addition series. When grown in monoculture, Idaho fescue from the undisturbed site produced almost twice as much shoot biomass as the disturbed-site populations averaged (Fig. 8.2). The addition of five cheatgrass seedlings resulted in reduced shoot biomass in the undisturbed population, but not in the populations from disturbed sites. Increasing cheatgrass density further still reduced production in all Idaho fescue.

![Figure 8.2 Shoot biomass of Idaho fescue from disturbed and undisturbed populations grown in addition series with cheatgrass. From Nasri (1993).](image-url)
The pattern did not change when the responses of five populations were considered individually (Table 8.3). Shoot biomass did not differ among the four disturbed-site populations at cheatgrass densities of zero and five seedlings per pot. Increasing cheatgrass density to 10 seedlings per pot resulted in significant, but equal, reduction in shoot biomass for all four disturbed-site populations. Shoot biomass decreased with increasing cheatgrass density in the undisturbed population. Idaho fescue from the undisturbed site produced significantly more shoot biomass when grown without cheatgrass interference than did Idaho fescue from the disturbed sites.

Table 8.3 Aboveground biomass (g) of Idaho fescue seedlings from five populations grown in an addition series with cheatgrass. From Nasri (1993).

<table>
<thead>
<tr>
<th>Ratio²</th>
<th>Combs Flat</th>
<th>Lone Pine</th>
<th>Blanchard</th>
<th>McCoin</th>
<th>Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:0</td>
<td>0.2656 aA</td>
<td>0.2906 aA</td>
<td>0.3303 aA</td>
<td>0.3261 aA</td>
<td>0.5666 bA</td>
</tr>
<tr>
<td>1:5</td>
<td>0.3639 aA</td>
<td>0.3442 aA</td>
<td>0.3619 aA</td>
<td>0.3391 aA</td>
<td>0.3712 aB</td>
</tr>
<tr>
<td>1:10</td>
<td>0.2115 aB</td>
<td>0.2110 aB</td>
<td>0.2213 aB</td>
<td>0.2042 aB</td>
<td>0.2467 aC</td>
</tr>
</tbody>
</table>

1. Within a row, different lower case letters indicate significant differences (α=0.05). Within a column, different upper case letters indicate significant differences. 2. Ratio of Idaho fescue seedlings to cheatgrass seedlings. 3. The first four populations are found on disturbed sites; the Island population is from an undisturbed relict area.

The constant shoot biomass of disturbed-site Idaho fescue when in grown in monoculture or the low cheatgrass density could be interpreted as evidence of greater competitive ability, but that would be incorrect. Competition occurs when neighboring plants attempt to sequester the same “quantum of light, ion of mineral nutrient, molecule of water, or volume of space” (Grime 1973). A successful
competitor captures the resource; the unsuccessful competitor achieves less growth, carbohydrate storage, or seed production as a result (Keddy 1989). Uptake is a function of the amount, activity, and distribution of resource-absorbing organs (Grime 1979) and resource capture and competitive success increase with leaf and root surface area (Weiner 1985; Harris 1967). The capacity for rapid production of roots and leaves, and quick morphological adjustment in response to transient resource enrichment, confers competitive ability (Grime 1979). A plant with a competitor's genotype would be expected to produce a lot of biomass quickly when grown without interference, as did Idaho fescue from the undisturbed site relative to disturbed-site Idaho fescue. A slow, largely invariable rate of growth is a trait of stress-tolerant plants. The constant shoot biomass of disturbed-site Idaho fescue is evidence of stress tolerance, as is the pattern of root growth (coarse exploration of a large volume of soil).

Idaho fescue has not persisted on grazed and invaded rangelands because of greater competitive ability in the enduring populations. More likely, these populations represent ecotypes that are more stress tolerant than their ancestral populations.

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APPENDIX

SCIENTIFIC AND COMMON NAMES OF PLANTS

IN THIS THESIS
<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em> L.</td>
<td>yarrow</td>
</tr>
<tr>
<td><em>Agropyron cristatum</em> (L.) Gaertner</td>
<td>crested wheatgrass</td>
</tr>
<tr>
<td><em>Agropyron desertorum</em> (Fisch. ex Link) Schultes</td>
<td>‘Nordan’ crested wheatgrass</td>
</tr>
<tr>
<td><em>Agropyron intermedium</em> (Host) Beauv.</td>
<td>intermediate wheatgrass</td>
</tr>
<tr>
<td><em>Agropyron spicatum</em> (Pursh.) Scribn. &amp; Smith</td>
<td>bluebunch wheatgrass</td>
</tr>
<tr>
<td><em>Amelanchier alnifolia</em> (Nutt.) Nutt.</td>
<td>serviceberry</td>
</tr>
<tr>
<td><em>Arabis</em> sp.</td>
<td>rockcress</td>
</tr>
<tr>
<td><em>Artemisia tridentata ssp. tridentata</em> Nutt.</td>
<td>(basin) big sagebrush</td>
</tr>
<tr>
<td><em>Artemisia tridentata ssp. wyomingensis</em> Beetle &amp; Young</td>
<td>Wyoming big sagebrush</td>
</tr>
<tr>
<td><em>Artemisia tridentata ssp. vaseyana</em> (Rydb.) Beetle</td>
<td>mountain big sagebrush</td>
</tr>
<tr>
<td><em>Astragalus</em> spp.</td>
<td>milkvetch, locoweed</td>
</tr>
<tr>
<td><em>Avena fatua</em> L.</td>
<td>wild oat</td>
</tr>
<tr>
<td><em>Bromus comutatus</em> Schrad.</td>
<td>hairy brome</td>
</tr>
<tr>
<td><em>Bromus mollis</em> L.</td>
<td>soft brome</td>
</tr>
<tr>
<td><em>Bromus rigidus</em> Roth</td>
<td>ripgut brome</td>
</tr>
<tr>
<td><em>Bromus rubens</em> L.</td>
<td>foxtail brome</td>
</tr>
<tr>
<td><em>Bromus tectorum</em> L.</td>
<td>cheatgrass, downy brome</td>
</tr>
<tr>
<td><em>Chrysothamnus nauseosus</em> (Pall.) Britt.</td>
<td>gray rabbitbrush</td>
</tr>
<tr>
<td><em>Chrysothamnus vicitiflorus</em> (Hook.) Nutt.</td>
<td>green rabbitbrush</td>
</tr>
<tr>
<td><em>Cryptantha</em> spp.</td>
<td>cryptantha</td>
</tr>
<tr>
<td><em>Eriogonum vimineum</em> Dougl.</td>
<td>broom buckwheat</td>
</tr>
<tr>
<td><em>Festuca idahoensis</em> Elmer</td>
<td>Idaho fescue</td>
</tr>
<tr>
<td><em>Festuca scabrella</em> Torr</td>
<td>rough fescue</td>
</tr>
<tr>
<td><em>Festuca ovina</em> L.</td>
<td>sheep fescue</td>
</tr>
<tr>
<td><em>Holosteum umbellatum</em> L.</td>
<td>holosteum</td>
</tr>
<tr>
<td><em>Juniperus occidentalis</em> Hook.</td>
<td>western juniper</td>
</tr>
<tr>
<td><em>Koeleria cristata</em> Pers.</td>
<td>junegrass</td>
</tr>
<tr>
<td><em>Lactuca sativa</em> L.</td>
<td>lettuce</td>
</tr>
<tr>
<td><em>Lepidium perfoliatum</em> L.</td>
<td>pepperweed</td>
</tr>
<tr>
<td><em>Lomatium</em> spp.</td>
<td>lomatium</td>
</tr>
<tr>
<td><em>Lupinus</em> spp.</td>
<td>lupine</td>
</tr>
<tr>
<td><em>Phlox</em> spp.</td>
<td>phlox</td>
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<tr>
<td><em>Poa secunda</em> Presl</td>
<td>Sandberg’s bluegrass</td>
</tr>
<tr>
<td><em>Poa cusickii</em> Vasey</td>
<td>Cusick’s bluegrass</td>
</tr>
<tr>
<td><em>Polygonum heterosepalum</em> Peck &amp; Ownby</td>
<td>dwarf desert knotweed</td>
</tr>
<tr>
<td><em>Purshia tridentata</em> (Pursh.) DC</td>
<td>bitterbrush</td>
</tr>
<tr>
<td><em>Raphanus raphistrum</em> (L.)</td>
<td>wild radish</td>
</tr>
<tr>
<td><em>Ribes cereum</em> Dougl.</td>
<td>wax currant</td>
</tr>
<tr>
<td><em>Rosa</em> spp.</td>
<td>rose</td>
</tr>
<tr>
<td><em>Salsola iberica</em> Sennen &amp; Pau</td>
<td>Russian thistle</td>
</tr>
<tr>
<td><em>Sisymbrium altissimum</em> (L.)</td>
<td>tumble mustard</td>
</tr>
<tr>
<td><em>Sitanian hystrix</em> (Nutt.) J.G. Smith</td>
<td>squirreltail</td>
</tr>
<tr>
<td><em>Sorghum halepense</em> (L.)</td>
<td>Johnsongrass</td>
</tr>
<tr>
<td>Scientific Name</td>
<td>Common Name</td>
</tr>
<tr>
<td>-------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td><em>Stipa columbiana</em></td>
<td>Columbia needlegrass</td>
</tr>
<tr>
<td><em>Stipa comata</em></td>
<td>needle-and-thread</td>
</tr>
<tr>
<td><em>Stipa thurberiana</em></td>
<td>Thurber’s needlegrass</td>
</tr>
<tr>
<td><em>Symphoricarpos albus</em></td>
<td>snowberry</td>
</tr>
<tr>
<td><em>Taeniatherum asperum</em></td>
<td>medusahead</td>
</tr>
<tr>
<td><em>Vulpia bromoides</em></td>
<td>vulpia</td>
</tr>
<tr>
<td><em>Vulpia octoflora</em></td>
<td>six-weeks fescue</td>
</tr>
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</table>