Spacing and Competition Between Planted Grass Plugs and Preexisting Perennial Grasses in a Restoration Site in Oregon

Russell T. Huddleston[1,2] and Truman P. Young[1,3]

Abstract

Planting native species into restoration settings where other natives already occur is a common practice. However, the competitive consequences of such plantings are rarely studied. Planting density also affects restoration costs. Here we examined the effects of established individuals of Lemmon's needlegrass (*Achnatherum lemmonii*) on plugs of bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) in a restoration site in Oregon. All three of these grasses are local native perennials. Plugs were planted at 6, 12, and 18 cm from established *A. lemmonii* bunchgrasses and also in plots without *A. lemmonii* neighbors. Plug survival was uniformly high, averaging more than 98%. Plugs planted at 6 cm from established grasses showed significantly lower growth and reproduction than plugs planted at 18 cm, which had similar values to plugs not planted in the vicinity of *A. lemmonii*. These results suggest that interplanting distances of as little as 18 cm were sufficient to greatly reduce competitive effects on newly planted plugs, at least in early establishment at this site.

Key words: **Agate Desert, interspecific competition perennial bunchgrass, planting density.**

Introduction

Restoration of plant communities requires an understanding of the mechanisms responsible for community structure and dynamics (Holmes & Richardson 1999). Competition between native plants and invasive exotics often limits the success of restoration efforts (Dyer & Rice 1999; Brooks 2000; Brown & Rice 2000; Carlsen et al. 2000; Green & Galatowitsch 2002; see review by Levine et al. 2003).

In some cases, intraspecific and interspecific competition among native species may also negatively affect the success of restoration projects. The effects of intraspecific plant spacing and density have often been examined in the context of agricultural production and forestry (reviewed in Harper 1977). Increased planting density is associated with decreased survival, biomass, and reproduction (Gubbels & Dedio 1990; Jefferson & Kielly 1998; Leitch & Sahi 1999; Otsamo 2002). Manipulating plant density in natural populations also affects individual success (e.g., Maron 2001; Rao et al. 2003). However, the effect of competition from existing native plants on restoration plantings is largely unstudied.

Native bunchgrass communities often contain several competing perennial grass species (Bazzaz & Parrish 1982). Competitive interactions in Midwest prairies were more intense between conspecific neighbors and species with similar growth habits than between species differing significantly in morphology (Goldberg 1987). In addition, these competitive interactions may be strongly dependent on the abundance and size of the neighboring plants (Goldberg 1987; Laterra et al. 1997). However, in a California grassland, interspecific competition with annual grasses resulted in significantly greater negative effects on growth and reproduction of the native perennial grass *Nassella pulchra* than did intraspecific competition, even in the highest intraspecific densities (Dyer & Rice 1999). The effects of intraspecific competition in *N. pulchra* only became apparent once competition from annual neighbors was eliminated (Dyer & Rice 1999).

Gap size in natural systems is often positively associated with the success of seedling establishment and persistence in grasslands, especially for species that are poor competitors for light and soil resources (Hitchmough et al. 1996; Morgan 1998). Davies et al. (1999), however, found that gap creation with herbicides had little effect on the long-term survival of transplanted native perennial grasses. Differing planting densities not only may affect planting success, but are also associated with very different planting costs, and therefore should be of interest to restoration practitioners. The few studies on the effects of planting density in restoration settings have shown both competitive (Brown & Rice 2000) and facilitative effects (Sheridan et al. 1998; Budelsky & Galatowitsch 2000). There have apparently been no studies on the effects of proximity to native neighbors on planting success in a restoration setting. This experiment was designed to examine how proximity of an established bunchgrass species affects the

[1]Department of Environmental Horticulture, University of California, Davis, CA 95616, U.S.A.
[2]Present address: CH2M Hill, 2485 Natomas Park Drive, Sacramento, CA 95833, U.S.A.
[3]Address correspondence to T. P. Young, email tpyoung@ucdavis.edu

initial growth and reproduction of two newly planted native grasses that share a similar growth form.

Study Site and Methods

Site

This study was carried out at the Agate Desert (42°25′ N, 122°52′ W) located in the central Rogue Valley of southwestern Oregon. The Agate Desert (elevation 400 m) is dominated by a landscape consisting of irregularly shaped soil mounds approximately 1 m high with low, often rocky areas between the mounds forming seasonal vernal pools. The area is underlaid by Agate Series soils. The surface layer is typically a loam about 15 cm thick underlaid with a clay loam. Effective rooting depth is 50–75 cm (SCS 1987).

The average annual precipitation for the area is 467 mm. Most of the precipitation falls during the months of November through March, with only 25% of the precipitation falling during the remaining 7 months of the year. The area received 419 mm of rain in 1999 and 478 mm in 2000. Monthly mean temperature ranges from 22.5°C in July to 3.2°C in December. Temperatures during the study period were similar to these means.

A 22-ha Nature Conservancy preserve is located in the northwestern part of the Agate Desert on the corner of Table Rock Road and West Antelope Road, Medford, Oregon, and is currently leased for winter cattle grazing. The previous vegetation of the Rogue Valley is largely conjectural but can be surmised from the remnant stands of native vegetation found in the foothills surrounding the valley. The vegetation of the Agate Desert was most likely a mixture of bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), and pine bluegrass (*Poa secunda*), with species such as Lemmon's needlegrass (*Achnatherum lemmonii*), squirreltail (*Elymus elymoides*), and California brome (*Bromus carinatus*) making up the earlier successional series. Nomenclature follows Hickman (1993).

The exotic annual grasses and forbs that currently dominate the nonpool areas of the mounded prairie throughout the Agate Desert largely replaced the native perennial grasses many decades ago, for reasons that are not clear, but may be related to the introduction of livestock and the arrival of invasive plants. Current vegetation was similar across our experimental plots. The non-native annual grass *Bromus hordeaceus* (soft chess) was the dominant cover in all areas with lesser amounts of *Taeniatherum caput-medusae* (medusahead) and *Vulpia myuros* (rattail fescue). Planted native *A. lemmonii* grasses (Lemmon's needlegrass) occurred at varying densities across the study area (see below). *Elymus elymoides* (squirreltail), a native perennial bunchgrass, was also present in some areas, but only as a minor component of the community. *Erodium cicutarium* (red-stem filaree) and the introduced clover *Trifolium dubium* (small-hop clover) were the most common and abundant forb species in all areas. Native forbs, such as *Plagiobothrys nothofulvus* (rusty popcornflower), *Lupinus bicolor* (miniature lupine), and *Lomatium utriculatum* (desert parsley), were also present in all of the plots.

Plugs

Festuca idahoensis and *P. spicata* seeds used in this experiment came from The Nature Conservancy's native plant propagation program, using seed collected from local remnant bunchgrass stands on the Agate Desert. A local native plant nursery, Plant Oregon, grew the plugs in a potting soil mixture in $5 \times 5 \times 13$–cm plastic containers, from seeds planted on 25 August 1999.

Experimental Design

Sixteen 1×5–m experimental plots were established in 1999 in the eastern portion of the preserve (an area of approximately 7 ha), which was burned and broadcast seeded with the native bunchgrass *A. lemmonii* in 1996 at a density of 400 seeds/m^2, followed by chain harrowing. No additional planting or burning was done before this study. The density of *A. lemmonii* across the site was highly variable at the time of the experiment. To capture the full range of established bunchgrass densities, experimental plots were stratified into four categories based on this natural variation: (1) high-density plots with 17–25 *A. lemmonii* plants/m^2; (2) medium-density plots with 13–14 plants/m^2; (3) low-density plots with 3–8 plants/m^2; and (4) plots with no established *A. lemmonii* plants. Plots with each density class were not contiguous, but rather interspersed with plots characterized by different densities, allowing their analysis as separate replicates. In each plot, a total of 18 seedlings, nine *F. idahoensis*, and nine *P. spicata* were planted. For each species in each plot, three plugs were planted at 18-, 12-, and 6-cm distances from an established *A. lemmonii* tussock, and nine plugs of each species were planted in plots containing no *A. lemmonii* plants. This arrangement allowed for the examination of neighbor proximity across the full range of *A. lemmonii* background density classes. In total, 288 plugs were planted.

The (2-month-old) plugs were planted on 31 October 1999. Holes were made using a 7.5-cm diameter auger to a depth of approximately 15 cm, so that the potting soil could be covered by a layer of soil to prevent desiccation. Soil was then tightly packed around the plugs. No additional fertilizer or water was added.

After planting, the location of each seedling was recorded within each plot. The initial basal diameter was measured at the widest part of the plant immediately above ground level. The initial tiller height was measured from the soil surface to the tip of the tallest tiller. The total number of *A. lemmonii* tussocks within each plot was counted. Plug condition, herbivory, and gopher activity in the vicinity of the plot areas were monitored throughout the experiment. On 10 and 14 June 2000, after seasonal growth had ceased, basal diameter and tiller height were remeasured, and the flowering culms produced by each plug were counted.

Soil samples were collected from each of the plots in November 1999. Five samples were randomly collected from each plot using a 2.5-cm diameter soil sampler to a depth of approximately 15 cm. The five samples were then homogenized into a single sample, dried, and sieved using a 2-mm screen. Samples were analyzed at the Division of Agriculture and Natural Resources analytical laboratory at the University of California, Davis, for organic matter (Walkley-Black), exchangeable (ammonium) potassium, extractible (Olsen) phosphorus, KCl-extractible soil nitrogen (NO_3 and NH_4), and soil texture.

Statistical Analysis

All data were analyzed using the SAS statistical software (Version 6.12; SAS Institute Inc. 1999). One-way analysis of variance (ANOVA) was used to determine whether there were any significant differences in the soil nutrients among the three density classes. Two-way ANOVA was used to analyze the effects of the distance classes and the areas differing in *A. lemmonii* background density on plug performance. Plug basal growth, tiller growth, and the total number of flowering culms were examined using two-way analyses of covariance with initial plug basal size used as a covariate, to determine whether there were any interactions between planting distance and background density of *A. lemmonii* on growth and reproduction. Square-root and log transformations were used as necessary to satisfy assumptions of normality. Post hoc comparisons among classes were done using a Tukey test for Honestly Significant Differences.

Results

Soils

There were no significant differences in the soils among the plots differing in *Achnatherum lemmonii* background density with respect to organic matter (range: 1.24–1.33%), potassium (127–139 ppm), phosphorus (12.2–16.5 ppm), extractible soil nitrate (2.3–3.2 ppm), or texture (all $p > 0.08$). The soils from all plots were classified as sandy loams, with less than 15% clay.

Transplant Survival

Transplant survival was high in all plots despite early evidence of herbivory on several of the plugs and extensive gopher activity throughout the study area. There was no mortality of either *Festuca idahoensis* or *Pseudoroegneria spicata* plugs in plots with high or medium densities of *A. lemmonii*. Extensive herbivory was observed on 12 of 18 plugs in one of the medium-density units in November 1999, but by June, all plants had fully recovered. Survival for *F. idahoensis* and *P. spicata* in the low-density plots was 97 and 92%, respectively. The locations of the missing transplants were within or immediately adjacent to fresh gopher tailings, suggesting that herbivory by pocket gophers, and not competition, was the likely reason for plug mortality. Despite considerable evidence of gopher activity in the plots without *A. lemmonii*, survival was 100% for *F. idahoensis* and 94% for *P. spicata*.

Plug Growth and Inflorescence Production at Differing Distances from Established Bunchgrasses

Plugs planted at a distance of 6 cm from an established needlegrass tussock exhibited half as much basal growth as did isolated plugs or plugs planted at distances of 12 or 18 cm for *F. idahoensis* ($F = 5.68$, $p < 0.001$) and distances of 18 cm for *P. spicata* ($F = 2.84$, $p = 0.04$; Fig. 1). Tillers of *F. idahoensis* planted at 6 cm were 23–38% taller than those planted further from established bunchgrasses or in isolation ($F = 5.90$, $p < 0.001$). Tiller height in *P. spicata* was not significantly affected by planting distance ($F = 2.08$, $p = 0.11$).

Reproduction also may be sensitive to proximity to competitors. Plugs of *P. spicata* planted at 18 cm from established *A. lemmonii* or as isolated plants produced up to twice as many flowering culms as those planted at 6 or 12 cm ($F = 3.11$, $p = 0.03$; Fig. 2). Plugs of *F. idahoensis* planted at 12 or 18 cm from established *A. lemmonii* or as isolated plants produced twice as many flowering culms as those planted at 6 cm ($F = 5.94$, $p = 0.008$; Fig. 2). All of these differences were similar across all the plots that differed in background *A. lemmonii* density. None of the main effects of plots with different *A. lemmonii* densities was significant (all $p \geq 0.08$).

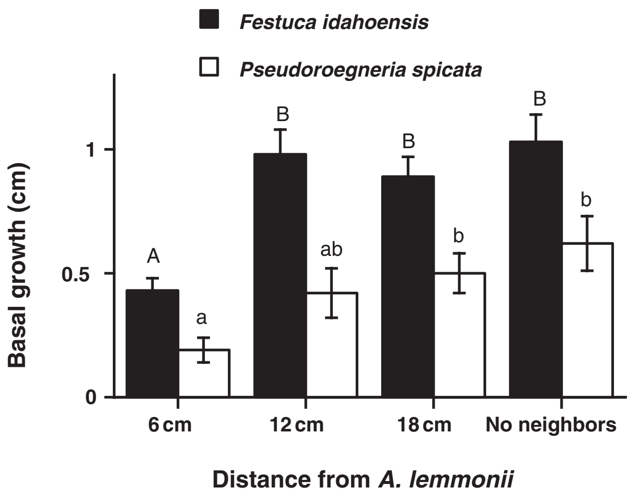

Figure 1. Basal growth between October 1999 and June 2000 of native grass plugs planted at different distances from established tussocks of *Achnatherum lemmonii*, and in sites without *A. lemmonii*. Within each species, bars sharing a letter did not differ significantly. Bars are one standard error.

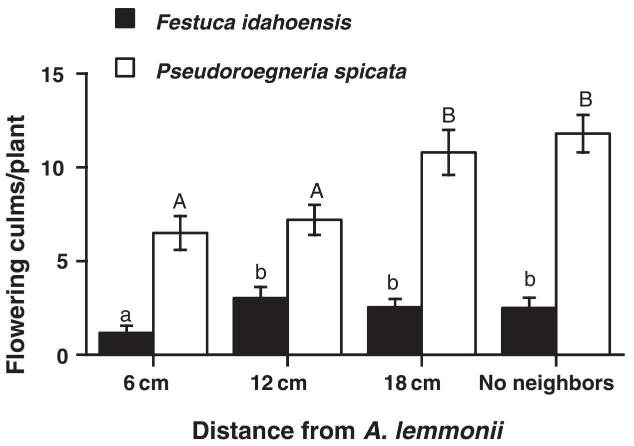

Figure 2. The mean number of flowering culms per plant in June 2000 of native grass plugs planted in October 1999 at different distances from established tussocks of *Achnatherum lemmonii*, and in sites without *A. lemmonii*. Within each species, bars sharing a letter did not differ significantly. Bars are one standard error.

Discussion

The effects of close proximity of planted grasses to established *Achnatherum lemmonii* tussocks were pronounced. Both *Pseudoroegneria spicata* and *Festuca idahoensis* had significantly reduced basal growth when planted 6 cm from an established bunchgrass tussock, compared to those plugs planted at a greater distance, or in areas without *A. lemmonii*. Competitive effects between neighboring plant species often result in morphological changes in root structure, tiller density, biomass, plant height, and basal area (Bazzaz & Parrish 1982; Kennett et al. 1992; Huber-Sannwald et al. 1996; Huber-Sannwald et al. 1997; Berntson & Wayne 2000).

Restoration success for many perennial species is often assessed in terms of vegetative growth and survival. However, long-term population viability also requires successful reproduction. Both species, planted in the fall of 1999, produced flowering culms in the summer of 2000. Even grasses planted in very close proximity had appreciable reproduction, but grasses planted closer to competitors exhibited greatly reduced inflorescence production.

Restoration scientists need to make informed decisions about planting densities and about planting proximity to potentially competing species. The results from this experiment suggest that the proximity of neighboring species does have an effect on initial plant growth and reproductive effort, especially when planted as close as 6 cm in this environment. We might expect the zone of interference to increase as planted grasses (and their competitors) increase in size, suggesting that even greater planting distances might be appropriate (although Hook & Lauenroth 1994 found that even mature bunchgrasses had limited competitive neighborhoods). On the other hand, planted perennials may be an effective suppressant of exotic annuals, and planting at initially high densities may have the benefit of initially holding space and enhancing overall population success in the face of competition from exotics (Budelsky & Galatowitsch 2000; Smit 2003), even if intraspecific competition eventually results in greater spacing.

In any case, it appears that the use of plugs can be an effective method of reintroducing native species to these degraded grasslands. This method may be particularly effective for species having a limited amount of seed available or those species having poor germination and initial survival in the field.

Planting 2-month-old native grass seedlings was a highly effective method of establishing *F. idahoensis* and *P. spicata* on this site. Previous restoration attempts with plugs on the Agate Desert suffered high mortality, apparently as a result of herbivory by pocket gophers (D. Borgias, The Nature Conservancy, May 1999, personal communication). In the present experiment, initial plug survival was unexpectedly high (>90%) despite early evidence of herbivory on several of the plants. The small amount of mortality observed was likely the result of herbivory from pocket gophers.

The improved survival of plugs and minimal herbivory from gophers were perhaps a result of the recent vegetation management on the preserve. Earlier (failed) restoration attempts involved planting plugs into a grassland community dominated by *Taeniatherum caput-medusae*, and lesser cover by forbs and other grasses. In contrast, the present experiment involved planting plugs into an area that had recently been burned and planted with native perennial bunchgrasses. As a result of the prescribed burn, the density of forbs had increased, *T. caput-medusae* cover had been reduced, and annual grasses such as *Bromus* spp. were more common (D. Borgias, The Nature Conservancy, May 1999, personal communication). Studies have found that pocket gophers prefer a diet of mostly forbs, supplemented with grasses such as *Bromus* and *Achnatherum* spp., but not *T. caput-medusae* (Keith et al. 1959; Burton & Black 1978). Therefore, the reintroduction of fire and native perennial *A. lemmonii* may have increased the amount of preferred forage for pocket gophers, which reduced herbivory on and increased survival of the native grass plugs. It is unlikely that fire reduced gopher populations (Masters et al. 1998).

The similarity in soils and associated vegetation among the experimental plots suggests that the variation in *A. lemmonii* density may be due to idiosyncratic differences in seeding rates, germination, and seedling survival not related to differences in environmental conditions across the site. In any case, there were no consistent differences in plug performance across plots differing in *A. lemmonii* density, after controlling for planting distance.

Our experimental planting distances appear to span an appropriate range for studying the question of competition. Perennial bunchgrass tussocks in natural grasslands are often separated by less than 15 cm, and established plants are likely to have strong interactions with neighbors in terms of resources acquisition (Hook et al. 1991; Aguilera & Lauenroth 1993). Hook and Lauenroth

(1994) found that *Bouteloua gracilis*, a native perennial grass in semiarid grassland, preempts resources within 10 cm from established plants, but is less able to obtain resources further away.

Huber-Sannwald et al. (1996) found both above- and belowground responses to competition in *P. spicata* when grown in association with *Agropyron desertorum*. Although belowground structures were not examined in this study, it seems likely that root morphology and distribution were also affected by the neighborhood interactions (Caldwell et al. 1991; Krannitz & Caldwell 1995).

An increase in tiller height with increasing proximity to shading competitors occurred in *F. idahoensis* despite a decrease in total aboveground biomass and reproduction. This is consistent with other studies that suggest competition for light is a major factor in this response (Gubbels & Dedio 1990; Naumburg et al. 2001; Fernandez et al. 2002).

Acknowledgments

We thank K. Rice, D. Borgias, M. Sullivan, H. Bolstad, K. Koehn, C. Riginos, K. Veblen, M. Huntzinger, D. Petersen, R. Smith, R. Evans, A. Berry, D. Pyke, and two anonymous reviewers for assistance of various kinds. This work was supported by The Nature Conservancy.

LITERATURE CITED

Aguilera, M. O., and W. K. Lauenroth. 1993. Neighborhood interactions in a natural population of the perennial bunchgrass *Bouteloua gracilis*. Oecologia **94:**595–602.

Bazzaz, F. A., and J. A. D. Parrish. 1982. Organization of grassland communities. Pages 233–254 in J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman.

Berntson, G. M., and P. M. Wayne. 2000. Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology **81:**1072–1085.

Brooks, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. American Midland Naturalist **144:**92–108.

Brown, C. S., and K. J. Rice. 2000. The mark of zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. Restoration Ecology **8:**10–17.

Budelsky, R. A., and S. M. Galatowitsch. 2000. Effects of water regime and competition on the establishment of a native sedge in restored wetlands. Journal of Applied Ecology **37:**971–985.

Burton, D. H., and H. C. Black. 1978. Feeding habits of Mazama pocket gophers in south-central Oregon. Journal of Wildlife Management **42:**383–390.

Caldwell, M. M., J. H. Manwaring, and S. L. Durham. 1991. The microscale distribution of neighboring plant roots in fertile soil microsites. Functional Ecology **5:**765–772.

Carlsen, T. M., J. W. Menke, and B. M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. Restoration Ecology **8:**18–29.

Davies, A., N. P. Dunnett, and T. Kendle. 1999. The importance of transplant size and gap width in the botanical enrichment of species-poor grasslands in Britain. Restoration Ecology **7:**271–280.

Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. Ecology **80:** 2697–2710.

Fernandez, M. E., J. E. Gyenge, G. Dalla Salda, and T. M. Schlichter. 2002. Silvopastoral systems in northwestern Patagonia I: growth and photosynthesis of *Stipa speciosa* under different levels of *Pinus ponderosa* cover. Agroforestry Systems **55:**27–35.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology **68:**1211–1223.

Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. Journal of Applied Ecology **39:**134–144.

Gubbels, G. H., and W. Dedio. 1990. Response of early-maturing sunflower hybrids to row spacing and plant density. Canadian Journal of Plant Science **70:**1169–1171.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Hickman, J. C., editor. 1993. The Jepson manual. University of California Press, Berkeley.

Hitchmough, J. D., H. Curtain, L. Hammersley, and J. Kellow. 1996. Effect of gap width and turf type on the establishment of the Australian forb *Bulbine bulbosa*. Restoration Ecology **4:**25–32.

Holmes, P. M., and D. M. Richardson. 1999. Protocols for restoration based on recruitment dynamics, community structure, and ecosystem function: perspectives from South African fynbos. Restoration Ecology **7:**215–230.

Hook, P. B., I. C. Burke, and W. K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual plant openings in North American shortgrass steppe. Plant and Soil **138:**247–256.

Hook, P. B., and W. K. Lauenroth. 1994. Root-system response of a perennial bunchgrass to neighborhood-scale soil–water heterogeneity. Functional Ecology **8:**738–745.

Huber-Sannwald, E., D. A. Pyke, and M. M. Caldwell. 1996. Morphological plasticity following species specific recognition and competition in two perennial grasses. American Journal of Botany **83:**919–931.

Huber-Sannwald, E., D. A. Pyke, and M. M. Caldwell. 1997. Perception of neighboring plants by rhizomes and roots: morphological manifestations of a colonial plant. Canadian Journal of Botany **75:**2146–2157.

Jefferson, P. G., and G. A. Kielly. 1998. Reevaluation of row spacing/plant density of seeded pasture grasses for the semiarid prairie. Canadian Journal of Plant Science **78:**257–264.

Keith, J. O., R. M. Hansen, and A. L. Ward. 1959. Effect of 2,4-D on abundance and foods of pocket gophers. Journal of Wildlife Management **23:**137–145.

Kennett, G. A., J. R. Lacey, C. A. Butt, K. M. Olson-Rutz, and M. R. Haferkamp. 1992. Effects of defoliation, shading and competition on spotted knapweed and bluebunch wheatgrass. Journal of Range Management **45:**363–369.

Krannitz, P. G., and M. M. Caldwell. 1995. Root growth responses of three Great Basin perennials to intra- and interspecific contact with other roots. Flora **190:**161–167.

Laterra, P., N. O. Maceira, and V. A. Deregibus. 1997. Neighbor influence on tiller demography of two perennial grasses. Journal of Vegetation Science **8:**361–368.

Leitch, M. H., and F. Sahi. 1999. The effect of plant spacing on growth and development in linseed. Annuals of Applied Biology **135:**529–534.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London. Series B. Biological Sciences **270:**775–781.

Maron, J. L. 2001. Intraspecific competition and subterranean herbivory: individual and interactive effects on bush lupine. Oikos **92:**178–186.

Masters, R. E., R. L. Lochmiller, S. T. McMurry, and G. A. Buckenhoffer. 1998. Small mammal response to pine-grassland restoration for red-cockaded woodpeckers. Wildlife Society Bulletin **26:**148–158.

Morgan, J. W. 1998. Importance of canopy gaps for recruitment of some forbs in *Themeda triandra*-dominated grasslands in south-eastern Australia. Australian Journal of Botany **46:**609–627.

Naumburg, E., L. E. DeWald, and T. E. Kolb. 2001. Shade responses of five grasses native to southwestern US *Pinus ponderosa* forests. Canadian Journal of Botany **79:**1001–1009.

Otsamo, A. 2002. Early effects of four fast-growing tree species and their planting density on ground vegetation in *Imperata* grasslands. New Forests **23:**1–17.

Rao, S. J., G. R. Iason, I. A. R. Hulbert, D. A. Elston, and P. A. Racey. 2003. The effect of sapling density, heather height and season on browsing by mountain hares on birch. Journal of Applied Ecology **40:**626–638.

SAS Institute Inc. 1999. SAS version 6.12. SAS Institute Inc., Cary, North Carolina.

SCS (Soil Conservation Service). 1987. Soil survey of Jackson County Area, Oregon. USDA Soil Conservation Service, Portland, Oregon.

Sheridan, P., G. McMahan, K. Hammerstrom, and W. Pulich. 1998. Factors affecting restoration of *Halodule wrightii* to Galveston Bay, Texas. Restoration Ecology **6:**144–158.

Smit, G. N. 2003. The importance of *Salvadora australis* in relation to tree thinning in preserving herbaceous plants in a semi-arid *Colophospermum mopane* savanna. Journal of Arid Environments **55:**483–501.