Establishing Native Grasses in a Big Sagebrush–Dominated Site: An Intermediate Restoration Step

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Abstract

Many semiarid rangelands in the Great Basin, U.S.A., are shifting dominance to woody species as a consequence of land degradation including intense livestock grazing and fire suppression. Whereas past rehabilitation efforts in Big sagebrush (*Artemisia tridentata*) steppes removed the shrub and added introduced forage grasses to successfully shift communities from shrublands to grasslands, current consensus is that native species should be included in restoration projects and that retention of some woody plants is desirable. We examined the potential for interseeding grasses into dense shrub communities as a precursor to thinning shrubs and releasing grasses from shrub interference. We compared seedling establishment of the native grass, Bluebunch wheatgrass (*Pseudoroegneria spicata*), with that of the Eurasia grass, Crested wheatgrass (*Agropyron desertorum*), in dense *Ar. tridentata* stands. Shrubs may play an important role as nurse plants for seedling establishment (reduced solar radiation, "island of fertility" effect) but result in highly contrasting light environments and root interference for seedlings. In experimental plots, we examined effects of *Ar. tridentata* shade levels (0, 40, 70, and 90% reduction of solar radiation) and initial root exclusion (present/absent) on the establishment and growth of *P. spicata* and *Ag. desertorum* seedlings. With this design we evaluated the interference effects of *Ar. tridentata* on the two grasses and identified the most beneficial microsites for grass restoration in *Ar. tridentata*–dominated communities. We predicted seedling survival and growth to be greater under moderate shade (40% reduction) and limited root competition than under no or strong shade conditions (0 and 90%) and unrestricted root interactions. Fifty to 85% of the *P. spicata* and *Ag. desertorum* seedlings survived the dry summer months of 1995 and 1996 and the intervening winter. Neither shading nor root exclusion from *Ar. tridentata* affected final seedling survival of either species. Seedling biomass of both grass species was negatively affected by initial root interactions with *Ar. tridentata*. However, the analysis of seedling biomass variability (coefficient of variation) indicated that in all shade and root-exclusion treatments, some seedlings of both species developed to large individuals to survive in *Ar. tridentata*–dominated rangelands. Thus, the use of interseeding techniques shows promise for restoring herbaceous species in dense *Ar. tridentata* stands and should be given further consideration when shrub retention is an important consideration.

Key words: *Agropyron desertorum*, *Artemisia tridentata*, degraded rangelands, native and introduced grass species, *Pseudoroegneria spicata*, restoration, shoot and root interference, survival.

Introduction

Under pre-settlement conditions, Big sagebrush (*Artemisia tridentata* (Nutt.)) and perennial tussock grasses, such as the widespread Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), codominated undisturbed sagebrush steppe communities (West 1991). Many semiarid plant communities in the Great Basin, U.S.A., are shifting to woody species dominance as a consequence of land degradation. The degradation is a consequence of both intense cattle grazing and fire suppression. Heavy grazing of grasses late in the growing season reduced the presence of grass in *Ar. tridentata* communities (Stoddart 1946; Young et al. 1977; West 1983) and removed the main source of continuous fuel for fires. When combined with the intentional suppression of fires, this overgrazing resulted in increase in dominance of species sensitive to fires and not preferred as forage for livestock, such as *Ar. tridentata* (Archer et al. 1988; Archer 1994; Miller et al. 1994; Van Auken 2000).

Sagebrush dominance was typical in the Great Basin during the 1950s when the Bureau of Land Management instituted programs to reduce sagebrush through herbicide applications and to rehabilitate lands by seeding introduced forage grasses such as the introduced tussock grass, Crested or Desert wheatgrass (*Agropyron desertorum* (Fisch. Ex Link) Schult. or *Ag. cristatum* (L.) Gaertn.) (Heady 1988). Thus, directed revegetation was considered necessary to reverse the transition to woody species dominance and to reintroduce tussock grasses into the ecosystem (Robertson 1971; Sanders & Voth 1983; West et al. 1984).

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Restoration of a diverse set of native plants is advocated to maintain a functioning ecosystem that provides forage and cover for a wide range of wildlife species. Some species, like the Greater Sage Grouse (*Centrocercus urophasianus*), require a mixture of sagebrush, grasses, and forbs for their survival (Crawford et al. 2004). Typical restoration plans in sagebrush grasslands call for the removal of shrubs to prepare for seeding herbaceous species using a rangeland seed drill (Vallentine 1989). We were interested in the potential of establishing tussock grasses directly into dense stands of sagebrush before applying treatments to reduce sagebrush densities and release grasses from interference for light and soil resources.

Artemisia tridentata may play a pivotal role for grass seedling establishment as nurse plants that reduce solar radiation and soil temperature and increase soil moisture and soil nutrient availability (Garcia-Moya & McKell 1970; Doescher et al. 1984; Schlesinger et al. 1990; Callaway 1995; Callaway et al. 1996; Chambers & Linnerooth 2001; Castro et al. 2002, 2004). Higher concentrations of soil organic matter beneath shrubs also may increase water-holding capacity and water retention. In addition, *Ar. tridentata* has been shown to move water vertically from deep to shallow soil depths via hydraulic lift (Caldwell & Richards 1989). Although mature grass neighbors do not require this water, they can access it (Caldwell 1990). Other species have shown beneficial responses from neighboring plant water (Caldwell et al. 1998), but to our knowledge, no one has examined seedling survival. Yet, hydraulically lifted water is also a limiting resource for which *Ar. tridentata* may compete for with understory plants (Campbell & Harris 1977).

Our major objective was to determine survival and growth of *P. spicata* and *Ag. desertorum* seedlings in the vicinity of *Ar. tridentata* and to examine if potential positive effects of shrubs on survival and growth may be counterbalanced by simultaneous adverse effects of shade and/or root interference for resources. We examined establishment and growth of seedling populations of the two grass species under different light levels (0, 40, 70, and 90% reduction of solar radiation) consisting of a combination of natural (beneath shrub canopy) and artificial (shade cloth) shade treatments in the vicinity of *Ar. tridentata* shrubs. We also evaluated how early belowground interference between the shrub and grass seedlings influenced these responses. We predicted that seedling survival and growth would be highest in treatments with intermediate shade and would decline with increasing and decreasing light availability. Further, we predicted that seedling survival and growth would be highest when roots of *Ar. tridentata* were excluded during the early phases of seedling establishment and growth.

Methods

This field experiment was conducted in 5-year-old *Artemisia tridentata* experimental plots near Logan, Utah (lat 41°45′N, long 111°48′W; 1,460 m a.s.l.). Plots consisted of a mixture of pure and hybrid forms of *A. t.* ssp. *vaseyana* (Rydb.) Beetle and *tridentata* Nutt., a common occurrence in foothill environments where both subspecies coexist (McArthur et al. 1988). The mean annual temperature in Logan, Utah, is approximately 8°C, and the mean daily maximum temperature is 31°C. Mean annual precipitation is 468 mm, with 75 mm falling in the summer months.

The distance between *Ar. tridentata* plants was approximately 50 cm in three blocks that captured the soil variation of the field location. On the north and south side of the shrubs (60–70 cm tall) eight grass seedling populations were planted in one of a combination of four shade and two root-exclusion treatments.

Shade Treatment

Artemisia tridentata plants vary in size and leaf density, and solar radiation may be considerably attenuated while passing through the shrub canopy. This results in reduced light availability beneath shrubs, especially on the north side of shrubs. By combining natural and artificial shade treatments, we established a "light gradient" consisting of 0, 40, 70, and 90% shade (light reduction) to simulate high- to low-light environments typically found in stands with different shrub densities. The south and north side of shrubs provided natural light treatments: south side 0% shade, north side 40% shade. To enhance light reduction beneath shrub canopies, as occurs in taller *Ar. tridentata* communities, artificial shade treatments were applied on the southwest side of shrubs (70% shade) and on the northwest side (90% shade). The gradient in photon flux density (PFD; μmol photons m^{-2} s^{-1}) ranged from approximately 1,500 (0% shade) to 120 (90% shade) μmol photons m^{-2} s^{-1} when measured at the four locations around shrubs at noon on several sunny days in May and September 1994 with a quantum sensor (LI-COR, Lincoln, Nebraska, U.S.A.) held horizontally on the soil surface. We chose shrubs of equal size to maintain similar light gradient conditions. Even though light conditions change throughout the growing season, the proportion of light reduction along the light gradient was maintained throughout the experiment. Any *Ar. tridentata* plant growing south of the target sagebrush that might cast a shadow on seeded grasses was tied back to eliminate shading. Artificial shade consisted of a combination of shade cloth and shade film that reduced PFD intensity but maintained the spectral composition of light typically found beneath canopies. The film consisted of a clear Mylar plastic covered with one sheet of window tint (3M Scotchtint Window Film NR20SMALL); it was sandwiched between two layers of standard chicken wire for support. The artificial shade formed a 40-cm-high half-cylinder around the west, south, and east side of a pair of grass seedling populations planted in root-exclusion tubes (see below) on the north and south side of the shrub. The shade construction remained open toward the north to minimize additional

microclimatic effects (e.g., temperature or wind) that could influence seedling growth. The shade construction provided morning and afternoon shade and partial sun exposure during noon in early May, the time of active growth. The artificial shade reduced the red:farred (R:FR) ratio from 1.03 in sunlight to 0.43–0.44 (measured with a Sky 660/730 sensor). Shading was removed during the winter months to avoid snow accumulation and altered freezing/thawing events.

Root-Exclusion Treatment

Root-exclusion tubes of different lengths make it possible to study the effects of early root interaction between adult plants and seedlings without having to remove competitors or to establish root trenches (Cook & Ratcliff 1984; Reichenberger & Pyke 1990). In fall 1994, two pairs of thin-walled polyvinyl chloride (PVC) tubes (3-mm thick) of two lengths (1 and 10 cm; 10-cm diameter) were pressed into the soil until the upper rim of the tube was flush with the surface and 20 cm from the stem of the target shrub. The distance between tubes in each pair was 4 cm. Because root density is highest in the upper 15 cm of the soil (Caldwell & Richards 1986), the 10-cm tubes provided root exclusion of neighboring *Ar. tridentata* plants during early seedling growth (Reichenberger & Pyke 1990). The root-exclusion tubes inhibited early competition between seedlings and adult shrubs but did not completely eliminate all potential positive or negative root effects of *Ar. tridentata* (redistribution of hydraulically lifted water, root exudation, etc.). PVC tubes did constrain horizontal water and nutrient flow in the upper soil layer. The 1-cm tubes served as controls where roots of grass seedlings interacted with those of neighboring *Ar. tridentata*, but inadvertent side effects of precipitation accumulation were similar among tube depths. In summer 1994, before root-exclusion tubes were inserted into the soil, 780 cm^3 of soil (the dimensions of the 10-cm-long tube) was excavated and sieved to eliminate rocks greater than 2 cm at each tube location. In a preliminary study, many seedlings died in root-exclusion tubes because large rocks inhibited seedling roots from accessing water beneath tubes. The sieved soil (including root material) was then used to refill the holes.

In fall 1994, 30 seeds of *Pseudoroegneria spicata* or *Agropyron desertorum* were sown into each tube. After germination, seedlings were thinned to 15 similar-sized individuals per tube, giving a density of about 1,900 seedlings/m^2. The density is similar to usual densities for *Ag. desertorum* but may be higher than natural densities for *P. spicata* (Pyke 1990). Each seedling within a tube was marked with a different colored wire hoop in April 1995 and monitored throughout the study. Seedlings emerging later were removed. Seedlings were monitored monthly for survival from April until October 1995 and from April until June 1996. In July 1996, shoots of each seedling were harvested by clipping at the soil surface; seedlings were then dried for 2 days at 70°C, and each individual seedling

was weighed. We determined the coefficient of variation (CV) for mass of individual seedlings in each tube to detect whether seedling size was homogeneous or whether some treatments yielded clear differences in seedling size within a population. Before harvest, we measured shoot height of the tallest tiller from the base to the insertion of the youngest leaf blade for each seedling. We determined mean tiller height and CV of height for seedling populations per tube.

Statistical Analysis

The experimental design was a randomized complete block, split–split plot design, with three replicated *Ar. tridentata* plots as blocks (wholeplots). There were three experimental units: block, location, and tube. In each block, there were three subsamples of randomly chosen shrubs for each grass species. The grass species were assigned to randomly chosen shrubs in the block subsamples. Each shrub contained all levels of each of two treatments, shade and root exclusion. Each shade level was split by the two root-exclusion levels. Subsample means were used in analyses. Analyses were conducted separately for each grass species. Individual seedling shoot biomass, maximum shoot biomass, shoot height, CV for biomass and height, and final seedling survival (%) were analyzed with the mixed procedure in SAS release 6.1 (SAS 1996). All variables were tested for normality with box plots and normal probability plots of residuals. Based on these tests, none of the variables had to be transformed. The data are presented as least square means (±SE) or model estimates from the mixed procedure. We conducted mean comparison tests for significant main and interaction effects using Bonferroni-adjusted *p* values. Survival analysis was conducted with the LIFETEST procedure. We also conducted multiple comparison tests of survival curves using the Wilcoxon rank statistic (Fox 2001).

Results

Survival

The highly contrasting light conditions in dense *Artemisia tridentata* communities did not affect the final survival of *Pseudoroegneria spicata* seedlings after the 20 months of the study (Fig. 1; shade main effect, $F_{[3,6]} = 1.86$; $p = 0.23$); however, there was some indication that seedling survival was lower with the two highest levels of shade. Fifty to 85% of the seedlings survived the three seasons: the dry summer months of 1995 and 1996 and the intervening winter period of 1995/1996. Early root interaction with *Ar. tridentata* did not influence final survival of *P. spicata* seedlings in any of the shade levels (Fig. 1; root-exclusion main effect, $F_{[1,8]} = 0.54$; $p > 0.48$). Survival of *P. spicata* seedlings from 21 April 1995 until 1 July 1996 was affected by shade levels and root exclusion (Fig. 2; log-rank test $\chi^2 = 42.56$, *df* = 7; $p < 0.001$). During the dry
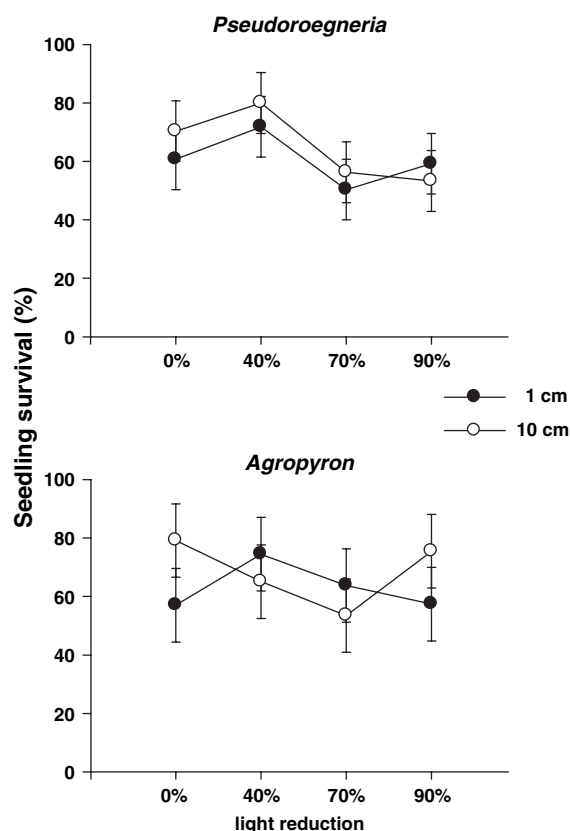
Figure 1. Least squares means (±SE) of survival (%) of
Pseudoroegneria spicata (top) and *Agropyron desertorum* (bottom)
seedlings by July 1996 in response to different shade (light reduction
0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia
tridentata* always present, 10 cm = roots of *Artemisia* absent at early
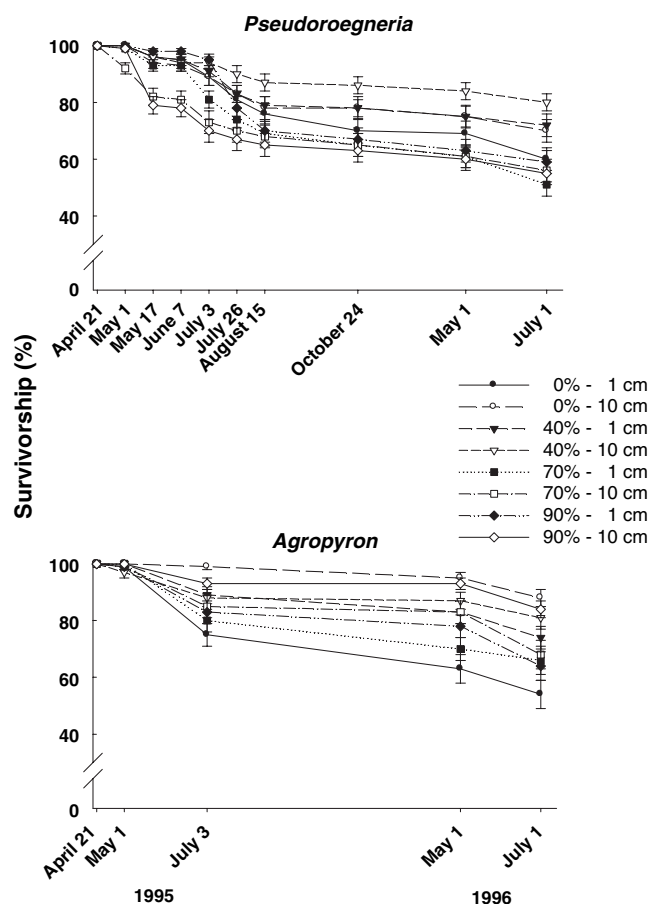stage) treatments.

Figure 2. Survivorship curves of *Pseudoroegneria spicata* (top) and
Agropyron desertorum (bottom) seedlings in response to different
shade (light reduction 0, 40, 70, and 90%) and root exclusion
(1 cm = roots of *Artemisia tridentata* always present, 10 cm = roots
of *Artemisia* absent at early stage) treatments over a 20-month time
period.

period from May to August 1995, the survival rate was
clearly higher for seedlings exposed to full light and mod-
erate light conditions compared to seedlings under strong
shade conditions (70 and 90% light reduction) where
approximately 20–35% of the *P. spicata* seedlings died
(Table 1: comparison 10 cm—0 vs. 70%; 10 cm—40 vs.
70%; 10 cm—40 vs. 90%; Fig. 2). However, in May and
June 1995 the survival rate was only low for those seed-
lings not interacting with *Ar. tridentata*, whereas by the
end of July 1995 all populations under dense shade had
lost 30% of their seedlings (Table 1: 90%—1 vs. 10 cm;
Fig. 2). Fall and winter of 1995/1996 hardly affected seed-
ling survivorship; in May and July 1996, 5–10% of the
seedlings died (Fig. 2).

Agropyron desertorum emerged as seedlings much ear-
lier in spring (March) 1995 than did *P. spicata*. However,
most of these seedlings died early due to frost heaving and
subsequent desiccation of their exposed roots. Neither
treatment affected the early mortality of *Ag. desertorum*
seedlings. Thus, the initial density of seedling populations
of *Ag. desertorum* consisted on average of 11 seedlings
(instead of 15). The percentage of surviving *Ag. deserto-
rum* seedlings by July 1996 was not affected by shade or

by early root exclusion of *Ar. tridentata* (Fig. 1; shade main
effect, $F_{[3,6]} = 0.50$, $p < 0.50$; root-exclusion main effect,
$F_{[1,8]} = 0.96$; $p < 0.36$). Survival rate of *Ag. desertorum*
seedlings over the 338 days was influenced by both shade
and root exclusion of *Ar. tridentata* (Fig. 2; $\chi^2 = 52.02$; $p <
0.0001$). The lowest survival rates occurred between May
and July 1995 and 1996. Under shade-free conditions,
seedling interactions with *Ar. tridentata* roots had the most
negative effect on seedling survival (Table 1: 0%—1 vs. 10
cm; Fig. 2). A similar root-exclusion response occurred
under the highest shade level (Table 1: 90%—1 vs. 10 cm;
Fig. 2). When interacting with *Ar. tridentata* roots and
moderate shading significantly benefited seedling survival
rate (Table 1: 1 cm—0 vs. 40%), especially in the second
year.

Biomass

Although early root exclusion did not affect the survival
of *P. spicata* seedlings, it resulted in higher mean shoot

Table 1. Multiple comparison of survivorship curves for *Pseudoroegneria spicata* and *Agropyron desertorum* seedlings based on Wilcoxon rank statistics with adjusted *Z* values.

	Pseudoroegneria spicata		*Agropyron desertorum*	
	Z	p <	Z	p <
Root-exclusion effect				
0%—1 vs. 10 cm	1.2272	0.220	5.7882	0.001
40%—1 vs. 10 cm	1.3386	0.181	0.8502	0.395
70%—1 vs. 10 cm	0.0176	0.986	0.9043	0.366
90%—1 vs. 10 cm	1.9662	0.049	3.4424	0.001
Shade effect				
Without root exclusion				
1 cm—0 vs. 40%	1.4938	0.135	3.2662	0.001
1 cm—0 vs. 70%	1.7151	0.086	1.6478	0.100
1 cm—0 vs. 90%	0.1998	0.842	1.3762	0.169
1 cm—40 vs. 70%	3.2214	0.001	1.6162	0.106
1 cm—40 vs. 90%	1.6917	0.091	1.7748	0.076
1 cm—70 vs. 90%	1.5112	0.131	0.2129	0.831
With root exclusion				
10 cm—0 vs. 40%	1.6077	0.108	1.6597	0.097
10 cm—0 vs. 70%	2.9829	0.003	3.4961	0.001
10 cm—0 vs. 90%	3.4237	0.001	0.6623	0.510
10 cm—40 vs. 70%	4.6112	0.001	1.7588	0.079
10 cm—40 vs. 90%	5.0340	0.001	0.9476	0.343
10 cm—70 vs. 90%	0.4702	0.638	2.6914	0.007

Shade treatments are light reduction: 0, 40, 70, and 90%; root-exclusion treatments are 1 cm = *Artemisia tridentata* roots always present, 10 cm = *Artemisia* roots absent at early stage.

biomass of seedlings regardless of shade levels (Fig. 3; root-exclusion main effect, $F_{[1,8]} = 109.31$; $p < 0.001$). The different shade conditions did not affect seedling biomass (Fig. 3; shade main effect, $F_{[3,6]} = 3.13$; $p < 0.12$). Overall, the CV of seedling mass in populations was greater when seedlings competed with *Ar. tridentata* roots compared to limited root interaction (Fig. 4; root-exclusion main effect, $F_{[1,8]} = 5.63$; $p < 0.04$). This suggests that only a few seedlings developed into large individuals when competing with *Ar. tridentata*. The largest mean seedling biomass occurred in the early root-exclusion treatment (Table 2; root-exclusion main effect, $F_{[1,8]} = 35.8$; $p < 0.0003$), and shading did not affect maximum seedling size (Table 2; $F_{[3,6]} = 1.86$; $p < 0.24$).

For *Ag. desertorum*, only early root exclusion decreased mean seedling mass (Fig. 3; root-exclusion main effect, $F_{[1,8]} = 7.93$; $p < 0.02$), whereas the different shade conditions had no effect (Fig. 3; shade main effect, $F_{[3,6]} = 7.93$; $p < 0.41$). The CV for individual seedling mass was high, yet it was not influenced by root exclusion of *Ar. tridentata* or shade conditions (Fig. 4; root-exclusion main effect, $F_{[1,8]} = 0.16$; $p > 0.7$; shade main effect, $F_{[3,6]} = 2.82$; $p < 0.13$). However, there was some indication that the CV of seedling mass was higher in the 90% light reduction treatment compared to the 40 and 70% reduction treatments (shade × root exclusion interaction, $F_{[3,8]} = 2.35$; $p < 0.15$). Neither the root exclusion nor the shade treatments affected mean maximum seedling size (Table 2; root-

exclusion main effect, $F_{[3,6]} = 0.60$; $p < 0.92$; shade main effect, $F_{[1,8]} = 0.01$; $p < 0.64$).

Shoot Morphology

Like mean shoot biomass of *P. spicata* seedlings, mean shoot height was greater when roots of *Ar. tridentata* were excluded (Fig. 5; root-exclusion main effect, $F_{[1,8]} = 21.95$; $p < 0.002$). The different shade conditions did not affect seedling height (Fig. 5; shade main effect, $F_{[3,6]} = 3.01$; $p < 0.12$), although with increasing shade, height seemed elongated. The CV of mean height was around 30% for all shade and root-exclusion treatments (Fig. 6; shade main effect, $F_{[3,6]} = 2.14$; $p < 0.20$; root-exclusion main effect, $F_{[1,8]} = 2.33$; $p < 0.16$).

Agropyron desertorum seedlings were shorter when exposed to roots of *Ar. tridentata* than when roots were excluded (Fig. 5; root-exclusion main effect, $F_{[1,8]} = 18.37$; $p < 0.003$). Seedlings growing under strong shade (70 and 90%) were on average 4 cm taller than unshaded and moderately shaded (40%) seedlings (Fig. 5; shade main effect, $F_{[3,6]} = 19.34$; $p < 0.002$). The CV of height for *Ag. desertorum* seedlings was similar (approximately 40%) for all combinations of root exclusion and shade
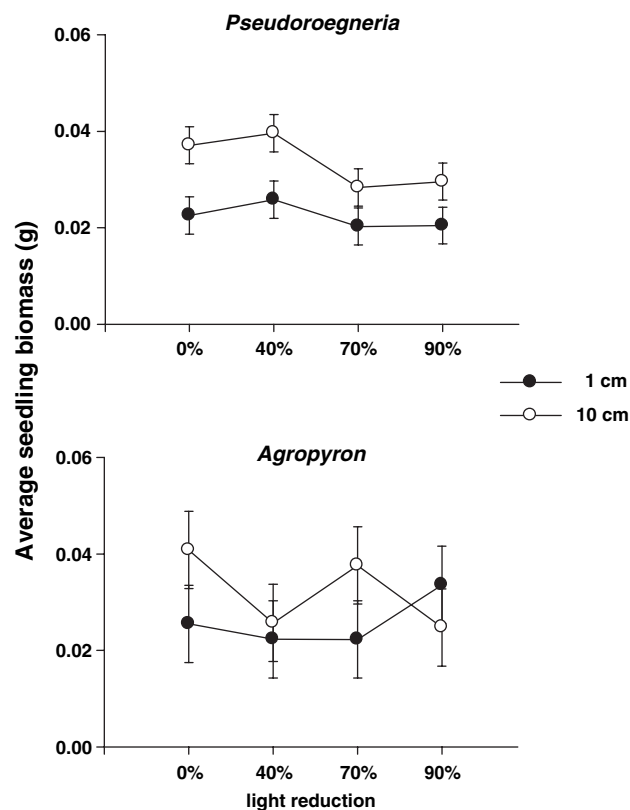

Figure 3. Least squares means (±SE) of shoot biomass (g) of *Pseudoroegneria spicata* (top) and *Agropyron desertorum* (bottom) seedlings in response to different shade (light reduction 0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia tridentata* always present, 10 cm = roots of *Artemisia* absent at early stage) treatments.

(Fig. 6; root-exclusion main effect, $F_{[1,8]} = 1.07$; $p < 0.33$; shade main effect, $F_{[3,6]} = 1.22$; $p < 0.38$).

Discussion

The area in the immediate vicinity of *Artemisia tridentata* shrubs presents a number of potentially favorable and adverse microsites for seedling establishment. Highly contrasting light environments on the south or north side of shrubs and the high soil resource availability beneath shrubs could both enhance (less heat stress, more soil resources) and hamper (insufficient irradiance, root exclusion between seedlings and shrub) seedling success. The use of shrubs as nurse plants is a useful tool in revegetation efforts in desert, mediterranean, and mountain ecosystems (Callaway et al. 1996; Castro et al. 2002, 2004). Thus, identifying the positive and negative effects of the abundant *Ar. tridentata* shrubs in the Great Basin may prove extremely valuable for low-input restoration efforts to reestablish perennial grasses in near monocultures of *Ar. tridentata*. This may prove important considering the loss of *Ar. tridentata* in the region and its impact through
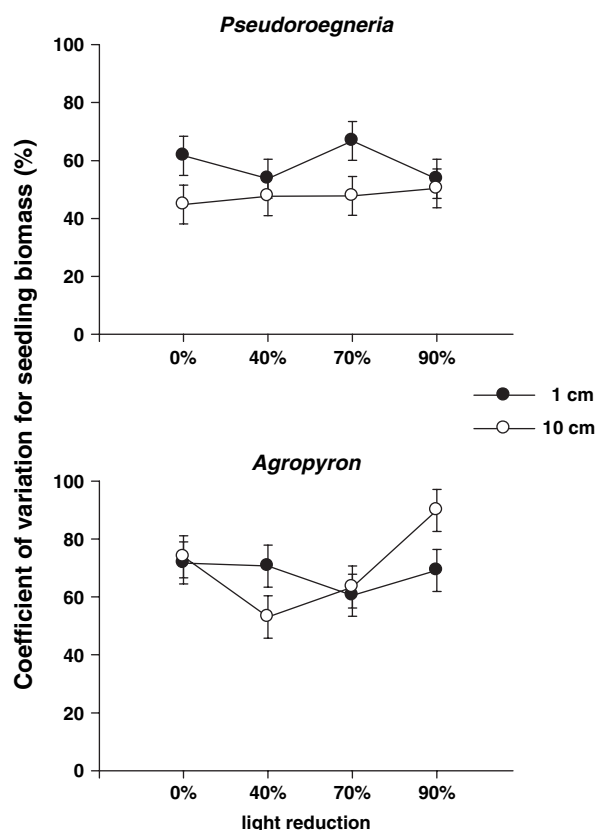
Table 2. Least squares means (±SE) of mean maximum shoot biomass (g) of *Pseudoroegneria spicata* and *Agropyron desertorum* seedlings after 20 months of growth under different shade (light reduction 0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia tridentata* present, 10 cm = roots of *Artemisia* absent at early stage) treatments.

Shade (%)	Root Exclusion (cm)	Treatments	
		Pseudoroegneria spicata	*Agropyron desertorum*
0	1	0.027 ± 0.006	0.041 ± 0.0142
0	10	0.043 ± 0.006	0.055 ± 0.0140
40	1	0.034 ± 0.006	0.029 ± 0.0142
40	10	0.056 ± 0.006	0.031 ± 0.0142
70	1	0.034 ± 0.006	0.039 ± 0.0142
70	10	0.043 ± 0.006	0.044 ± 0.0142
90	1	0.024 ± 0.006	0.057 ± 0.0142
90	10	0.042 ± 0.006	0.032 ± 0.0142

trophic systems (Knick et al. 2003). Restoration techniques are needed that can retain the remaining *Ar. tridentata* while restoring the depleted herbaceous community. Establishing grasses in association with *Ar. tridentata* and then using techniques such as mosaic fires or low levels of herbicides to thin sagebrush might achieve this goal (Johnson et al. 1996; Wrobleski & Kauffman 2003).

Contrary to our prediction, ultimate seedling survival of *Pseudoroegneria spicata* and *Agropyron desertorum* was not affected by root interference with *Ar. tridentata* although timing of mortality in the first year was influenced. Survival of seedling populations of *P. spicata* and *Ag. desertorum* after 20 months was high in the relatively dense *Ar. tridentata* stands used for this study. On average, 75% of the seedlings of both grass species survived, indicating that the light gradient caused by the canopy and early root interference of *Ar. tridentata* did not considerably affect the survival of either grass species. Evidence that seedling mortality in the first half of the experiment was not density dependent (intraspecific competition) is provided by the fact that seedlings with greater mean seedling biomass did not necessarily coincide with sparser populations. Factors associated with resource interference with *Ar. tridentata* are more likely the explanation. The first months of the growing season in 1995 was the period when seedling survival of *P. spicata* was negatively affected at locations where irradiance was the lowest. The decline in seedling survival was only observed initially (May and June 1995) in the absence of early interaction with *Ar. tridentata* roots, providing some indication of a negative nurse plant effect. By August 1995 the survival of all seedling populations exposed to 70 and 90% light reduction had declined to 70%.

It was probably a combination of light reduction and early water scarcity that affected seedling survival in summer of 1995. *Artemisia tridentata* hydraulically lifts water from greater root depths and redistributes water to shallow soil (Caldwell & Richards 1989), where it could
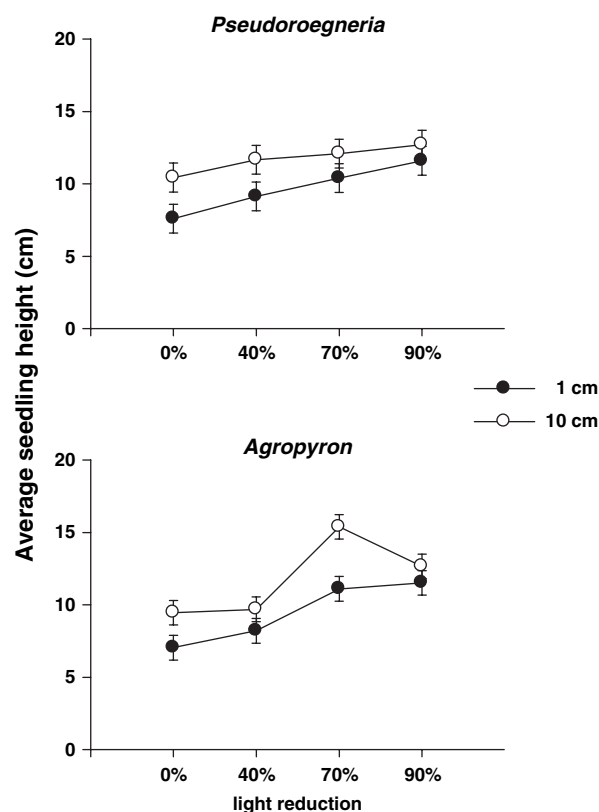

Figure 4. Least squares means (±SE) of CV for shoot biomass (%) of *Pseudoroegneria spicata* (top) and *Agropyron desertorum* (bottom) seedlings in response to different shade (light reduction 0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia tridentata* always present, 10 cm = roots of *Artemisia tridentata* absent at early stage) treatments.

Figure 5. Least squares means (±SE) of shoot height (cm) of *Pseudoroegneria spicata* (top) and *Agropyron desertorum* (bottom) seedlings in response to different shade (light reduction 0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia tridentata* always present, 10 cm = roots of *Artemisia* absent at early stage) treatments.

Figure 6. Least squares means (±SE) of CV for shoot height (%) of *Pseudoroegneria spicata* (top) and *Agropyron desertorum* (bottom) seedlings in response to different shade (light reduction 0, 40, 70, and 90%) and root exclusion (1 cm = roots of *Artemisia tridentata* always present, 10 cm = roots of *Artemisia* absent at early stage) treatments.

potentially become an important water source for seedlings growing beneath *Ar. tridentata* canopies. Dawson (1996) has shown this phenomenon is important for small trees that do not access deep water. Although hydraulic lift may be important for grass seedlings establishment, Caldwell (1990) demonstrated that for mature forms of these grasses it is only minor. Further research would need to determine the role of hydraulic lift in seedling establishment.

In contrast, *Ag. desertorum* seedling survival during the first months was negatively affected by early interactions with *Ar. tridentata* plants for almost all irradiance levels. This root interference effect on survival was most negative when seedlings were fully exposed to light. Survival was highest in the absence of early root interactions with *Ar. tridentata* in both heavily shaded (90%) and fully light-exposed grasses (0%) (Fig. 2), suggesting that the survival of *Ag. desertorum* seedlings is primarily affected by root interference with *Ar. tridentata*.

In a previous field study (Reichenberger & Pyke 1990), seedlings of the two grass species in the vicinity of *Ar. tridentata* ssp. *vaseyana* and *Ar. tridentata* ssp. *wyomingensis* shrubs died 3–5 months after the initiation of the experiment. This high mortality was probably caused by root competition between *Ar. tridentata* and the seedlings;
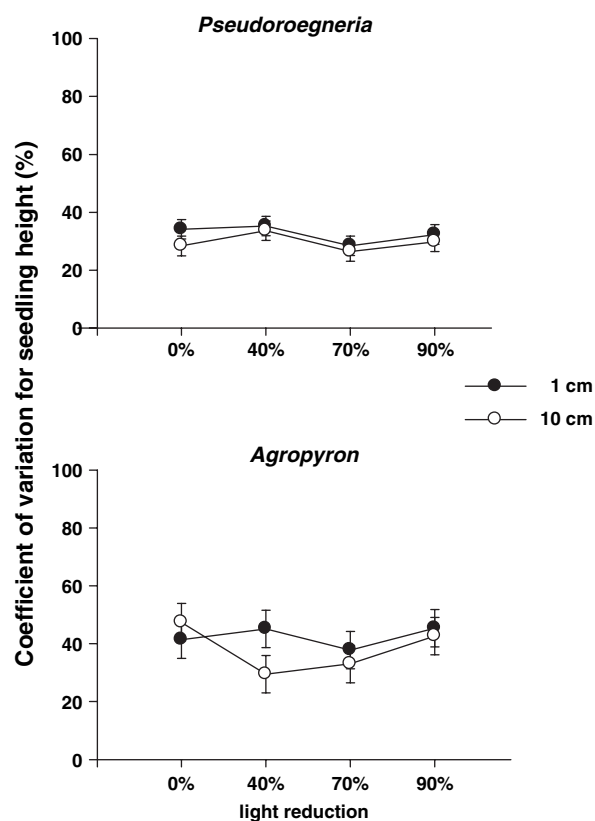
however, potential shading effects by *Ar. tridentata* on grass seedling performance were not examined. Similar to our study, early root interference decreased survival of *Ag. desertorum* seedlings, whereas the survival of *P. spicata* seedlings was not directly affected by root interaction with shrubs. Seedling survival in semiarid deserts of the Intermountain Region is primarily influenced by water availability during the growing season. Soil moisture is usually high early in the growing season and becomes increasingly limiting during the summer months, coinciding with the commonly high and low survival rates of seedlings of perennial species in these seasons (Salihi & Norton 1987; Pyke 1990; Reichenberger & Pyke 1990). We observed somewhat contrasting patterns of seedling survival for *Ag. desertorum* whose seedling survival was lowest between the beginning of May and early July in both years, whereas between July and September (the driest months) almost all seedlings survived. For *P. spicata*, decline in seedling survival was highest between June and the beginning of August. Water limitation was likely the most critical factor responsible for the high seedling mortality in the Reichenberger and Pyke study. Two factors likely influenced the outcomes of the two studies: (1) the long-term, average annual precipitation is higher (490 mm) at the Green Canyon Experimental Station

than in Curlew (305 mm), where the other study was conducted; (2) 1989/1990 were dry years, and 1995/1996 were relatively wet years. However, besides total annual precipitation and the size of individual precipitation events it is ultimately soil water pulses that are available for seedlings that translate precipitation into water usage (Reynolds et al. 2004). The importance of these water pulses (size, frequency, etc.) for seedling establishment, survival, and growth requires further investigation.

Another study indicated that soil water extraction rates of adult plants of the two grass species showed marked differences when interacting with *Ar. tridentata* plants, with *Ag. desertorum* being a much better competitor for water than *P. spicata* (Eissenstat & Caldwell 1988). Seedlings of *Ag. desertorum* do not seem to exhibit soil water extraction rates as high as adult plants when interacting with *Ar. tridentata* roots, indicating that other forms of interference may be involved (e.g., Callaway et al. 2004). This was shown in the previous study (Reichenberger & Pyke 1990) and in our study where we observed an early decline in *Ag. desertorum* seedling survival when interacting with adult *Ar. tridentata*.

Although *Ar. tridentata* does not appear to decrease seedling survival of the two grass species, root interactions negatively affect mean shoot biomass and height. A lack of early root interference with *Ar. tridentata* doubled mean seedling size of *P. spicata* under full light and moderate shade conditions, whereas low light conditions decreased seedling biomass due to limited availability of carbohydrates for root growth and resource uptake (Jackson & Caldwell 1992). *Agropyron desertorum* seedlings also were larger when released from early root interference with *Ar. tridentata*, although different light conditions did not indicate clear effects on seedling biomass. For long-term seedling survival, it is important to examine seedling size and thus the size distribution of seedling populations, because the likelihood for survival of a few yet vigorous seedlings may be substantially higher than for a larger number of relatively small seedlings (Schwinning 1996). However, these are predictions, which should be tested in long-term studies. Overall, the size variability was high in all seedling populations for both grass species, suggesting that a few large individuals occurred in all light and root interaction treatments. *Pseudoroegneria spicata* seedling populations had more pronounced size variability (high CV) in the early root-exclusion treatments, whereas *Ag. desertorum* seedling populations had overall a very high CV. The largest *P. spicata* seedlings occurred in early root-exclusion treatments, whereas the size of the largest *Ag. desertorum* seedlings did not depend on early root exclusion from *Ar. tridentata*.

Although in semiarid and arid environments, soil nutrient concentrations beneath shrub canopies are generally much higher than in interspaces due to the "island of fertility" effect, the spatial distribution of soil organic matter and soil-extractable phosphorous and potassium may show high spatial variability beneath *Ar. tridentata* shrubs (Jackson & Caldwell 1993). Although the shrubs in our study were only 5 years old and hence the island of fertility effect not as apparent, the few big seedlings may have been successful in garnering those soil resources; however, further studies will be needed to verify this assertion.

Most revegetation and restoration techniques for arid and semiarid rangelands require removal of woody vegetation before reintroducing the herbaceous components of the community. Our results indicate that reintroducing the herbaceous plants before reducing the abundance of the woody plants may be feasible and warrants further investigation. We did not detect marked differences between the two species in establishment, survival, or growth. Thus, the native *P. spicata* appears as suitable for restoration purposes as the introduced *Ag. desertorum*. Our results also indicate that when using *P. spicata* seeds for restoration purposes in dense *Ar. tridentata* stands, the light conditions should not affect seedling establishment and growth either positively or negatively unless light reduction is strong (70–90%). Thus, seeding on south sides of *Ar. tridentata* is recommended. Because root interaction with *Ar. tridentata* decreases mean seedling biomass, preference should be given to seeding in the transition of undershrub canopies and interspaces to minimize root interaction with *Ar. tridentata*. Thinning of *Ar. tridentata* stands using prescribed fire (Bunting et al. 1987; Wrobleski & Kauffman 2003) or selective herbicides (Johnson et al. 1996) 2–3 years after seeding may allow grass seedlings to mature into reproductive adults. This approach should promote the maintenance of a more competitive community, restore species and structural diversity, and thereby restrict the spread of exotic annuals more rapidly than traditional techniques requiring removal of shrubs followed by the application of shrub/grass seed mixtures. Based on this and a previous study (Reichenberger & Pyke 1990), the success rate of these types of restoration methods can vary significantly from year to year but may be as successful as or more successful than using seed drills in arid environments (Whisenant 2002).

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