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PINUS PONDEROSA SEEDLING ESTABLISHMENT AND THE INFLUENCE OF COMPETITION WITH THE BUNCHGRASS AGROPYRON SPICATUM

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Interspecific competition between *Agropyron spicatum* (Pursh.) Scrib. & Smith bunchgrasses and naturally established seedlings of *Pinus ponderosa* was examined within a pine/bunchgrass community. A wire mesh was used to separate bunchgrass culms from pine seedling shoots to determine if the bunchgrass canopy influenced the survival of pine seedlings. In addition, two lengths of root exclusion tubes were used to determine the effects of bunchgrass root overlap on pine seedlings. The bunchgrass canopy did not significantly affect pine seedling survival. However, root competition, presumably for water, significantly decreased pine seedling survival. Exclusion of bunchgrass roots from a 0.15-m- and 0.30-m-deep root zone of pine seedlings resulted in 40% and 80% reductions in mortality, respectively. Root exclusion also significantly delayed mortality 2–3 wk. Pine seedlings developed taproots that reached below the zone of maximum bunchgrass root density within 4 wk of germination. The pine/bunchgrass community is dominated by two species that utilize similar resource zones in the soil during the establishment of pine germinants in the bunchgrass understory. Interspecific competition tends to be greatest during this establishment stage and becomes reduced as pine seedlings grow and explore the deeper regions of the soil profile. In areas with shallow soils and an established bunchgrass understory, establishment of pine seedlings may occur successfully only if soil moisture is available in deeper soil horizons during the summer.

Introduction

Interspecific competition for limited resources can decrease growth and survival of species within a plant community and is an important process affecting plant community structure (Whittaker 1975; Harper 1977; Parrish and Bazzaz 1982; Tilman 1982; Newman 1983; Christy 1986; Miller and Werner 1987; Reichenberger and Pyke 1990). Use of limited resources by more competitive species can reduce resource availability for less competitive species (Tilman 1989) and may be especially pronounced when one species is in the seedling stage. In addition, early colonization and resource capture on sites with low productivity may exclude any new species or limit the growth and survival of existing species (Grime 1977, 1979). The detrimental effects of interspecific plant competition belowground for soil water, however, can be offset in some cases where shading by established vegetation may ameliorate the effects of intense solar radiation and associated high temperatures and evaporative demand limit plant function (Shreve 1931; Turner et al. 1966; Allen and Lee 1989; Belsky et al. 1989; Frost and McDougald 1989; Nobel 1989; Wilson 1989; Jacquart and Armentano 1992).

In semiarid and arid ecosystems of the western United States, plant competition for available soil water has been shown to influence species survival (Fonteyn and Mahall 1981; Robberecht et al. 1983; Allen and Allen 1986; Caldwell and Richards 1986; Caldwell 1988; Allen and Lee 1989; Gordon et al. 1989; Sala et al. 1989; Franco and Nobel 1990; Riegel et al. 1991), particularly when newly established seedlings compete

with established vegetation. Competition for water may also affect seedling survival on drier habitats within mesic forest ecosystems (Shainsky and Radosovich 1986, 1992; Peterson 1988). Associations of *Pinus ponderosa* (Dougl.) Lawson and *Agropyron spicatum*² (Pursh.) Scrib. & Smith persist on the drier sites that form ecotones between forests and grasslands and as seral communities in more mesic forest communities (Daubenmire 1943, 1968; Smith 1985; Cooper et al. 1987). This community is characterized by an open pine overstory and a well-developed bunchgrass understory with few other plant species present.

Pinus ponderosa is unique among tree species of the northwestern United States because it can survive on xeric sites where other trees are unable to establish naturally. This includes more mesic sites when disturbance has removed the existing forest overstory and understory vegetation, thereby creating a hotter, drier microenvironment (Riegel et al. 1992). *Pinus ponderosa* is thought to occupy this ecological niche because of a greater adaptability to xeric conditions than other tree species (Smith 1985). *Pinus ponderosa* trees have been shown to survive in areas with low precipitation by maintaining high water use efficiencies and deep root systems that utilize water sources unavailable to other plants (Daubenmire 1968; Jackson and Spomer 1979; DeLucia et al. 1988; DeLucia and Heckathorn 1989; DeLucia and Schlesinger 1991). These adaptations may also allow pine seedlings to establish in the highly competitive environment of a bunchgrass understory.

In northern Idaho spring germination of *P. ponderosa* seedlings on sites dominated by bunchgrasses is abundant, although few seedlings survive the environment of summer months (Cooper et al. 1987; P. F. Kolb

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²Proposed name change to *Pseudoroegneria spicata* (Pursh) Löve subsp. *spicata* (Barkworth and Dewey 1985).

and R. Robberecht, unpublished data). A primary cause of low seedling survival may result from interspecific competition for soil resources between bunchgrasses and tree seedlings. Species with fibrous root systems, such as *A. spicatum*, are better competitors for limited soil nutrients and particularly for mobile resources such as water (Caldwell and Richards 1986; Caldwell 1988; Eissenstat and Caldwell 1988; Gordon et al. 1989). We hypothesize that competition for soil resources, especially water, resulting from root overlap between pine seedlings and bunchgrasses limits pine seedling growth and survival. Alternatively, if tussocks of *A. spicatum* intercept a portion of the incoming solar radiation near newly established pine seedlings, these tussocks could ameliorate high soil surface and air temperatures that would otherwise be lethal to newly germinated pine seedlings. The objectives of this study were, therefore, to determine (1) the effects of belowground competition for water between *A. spicatum* and seedlings of *P. ponderosa*, (2) the relationship between pine seedling development and seasonal soil water availability, (3) the effects of depth of available soil water on seedling growth and carbon allocation, and (4) the influence of a bunchgrass overstory on the productivity and survival of pine seedlings.

Material and methods

FIELD

This study was conducted at Basalt Hill on the University of Idaho Experimental Forest (46°52'N, 116°47'W, 1100 m a.s.l.), 52 km northeast of Moscow, Idaho, in a seral *Pinus ponderosa*/*Agropyron spicatum* community composed of a mature *P. ponderosa* overstory of ca. 50 trees ha⁻¹ with a bunchgrass understory interspersed with shrubs and herbs. The soil is a Uvi-Spokane association (Barker 1981) silt loam ca. 0.5 m in depth overlying decomposing granite.

During two consecutive summer seasons, 30 newly germinated pine seedlings were randomly chosen in a homogeneous 1-ha area on a south-facing 15° slope. Three root treatments consisting of root exclusion tubes of multiple lengths (Cook and Ratcliff 1984; Snaydon and Howe 1986; Reichenberger and Pyke 1990) were used to exclude bunchgrass roots. For a control, 10 seedlings received no belowground manipulation and thus were exposed to root competition from bunchgrasses. For partial root competition, 0.15-m-long by 0.1-m-diameter stainless steel cylinders were inserted around another 10 pine seedlings. The majority of root competition from bunchgrasses was excluded by inserting 0.30-m-long by 0.1-m-diameter cylinders around the remaining 10 pine seedlings. The top of each cylinder was flush with the soil surface. Five seedlings from each of the three root treatments were randomly selected for the aboveground treatment, which consisted of a thin wire mesh placed around each pine seedling. This procedure separated bunchgrass culms from the pine seedling shoot within a 1 m² area. The remaining 15 pine seedlings without any bunchgrass culm manipulation served as the control group. An additional and separate group of 24 *P. ponderosa* seedlings located on the site were studied for root development over the growing season. Root development was determined biweekly by excavating three randomly selected seedlings. Pine seedlings that died in the root exclusion study were also

excavated. The number of needles, needle length, and stem diameter were measured weekly for all seedlings. Foliage and root areas were measured using a digital image analysis system (Decagon DIAS II). In addition, bunchgrass shoot and root density, number of germinating pine seedlings, visually estimated percentage of cover, and attenuation of solar radiation by bunchgrass canopies were measured in the 1 m² area around each selected seedling. Photosynthetically active radiation (PAR, 400–700 nm) was measured with a LI-COR model LI-190SA quantum sensor.

Seedling height, number of live needles, and the mortality of seedlings within a 1 m² area surrounding each treatment seedling were monitored weekly. Ambient soil water potential, soil water content, and temperature were also monitored weekly at three locations across the study site at depths of 0.05 m, 0.30 m, and 0.5 m with soil psychrometers (Wescor Corp. model PCT-55) and by gravimetric analysis. These three soil depths represented depths of root competition for each treatment. Air temperature and relative humidity 0.2 m above the ground were measured continuously throughout the summer with a hygrothermograph (Bendix model 594), which was calibrated monthly with an Assmann psychrometer. Stomatal conductance was measured monthly between 0800 and 1000 with a steady state porometer (LI-COR model LI-1600). The Bonferroni *t*-procedure ($\alpha = 0.05$, $c = 3$ [Dunn 1961]) was used to determine significant differences among treatment means. Correlation analysis was performed to determine the relationship between water potential, stomatal conductance for pine needles, and seedling mortality.

GREENHOUSE

Five 1-yr-old *P. ponderosa* seedlings, obtained from the University of Idaho Experimental Nursery, were grown for 2 mo in 0.15-m-diameter by 0.40-m deep cylindrical containers filled with commercial potting soil. They were watered weekly and fertilized with a 100 ppm solution of N-P-K (20%-20%-20% by mass) fertilizer. One month after the onset of needle growth, photosynthetic rates with respect to light level were determined for new foliage by enclosing seedling shoots in a cuvette attached to an open flow gas exchange system (Bingham et al. 1980) connected to an infrared gas analyzer (ADC model 225MK3) under a constant temperature of 25°C and a vapor density of 12 g m⁻³.

In addition, 25 *P. ponderosa* seedlings were planted shortly after germination in polystyrene cylinders 0.06 m diameter by 1.0 m in length and filled with washed sand to determine the influence of available water depth on stomatal conductance and seedling carbon allocation. Supplemental lighting was provided by metal halide lamps that produced a combined lamp and sun irradiance of 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ or greater over a 12-h photoperiod. All containers were initially watered to near saturation with a 500 ppm solution of N-P-K (20%-20%-20% by mass) fertilizer. Seedlings were then monitored for root growth by randomly choosing one seedling every week and excavating the root system. After seedling roots had penetrated the entire 1-m length of the container (3 wk), each of the 21 seedlings was randomly assigned to one of three treatments, consisting of a surface water supply only (top one-third of the container), 0.30-m water supply only (middle third), or 0.9-m water supply only (bottom third). From preliminary studies, we determined that 100 mL of water injected through a small hole in the container wall would be entirely held by the sand matrix suction in a 0.3-m section of the container. Stomatal conductance for whole seedlings was measured every other day at 10:00

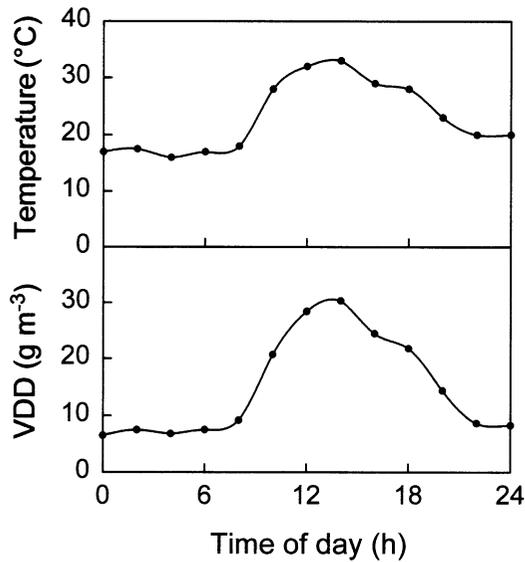


Fig. 1 Mean July–August diel temperatures and vapor density deficits (VDD) 0.20 m above the soil surface of the field study. Each point represents the mean of 20 samples, with standard errors of the mean ranging from 2.6% to 4.3%.

A.M. to determine seedling water stress. When the majority of the seedlings exhibited a 75% reduction in stomatal conductance, which had been previously determined to indicate imminent death, all seedlings were given 100 mL of water at their respective treatment depths. This process was followed through four watering cycles over 4 mo. Projected leaf area and leaf dry biomass, and root length and dry biomass in 0.3-m depth increments were determined at the end of the experiment. Differences in the means of shoot biomass, root biomass, and root biomass distribution were compared using the Bonferroni *t*-procedure ($\alpha = 0.05$).

Results

FIELD

The density of newly germinated seedlings of *Pinus ponderosa* on the 30 1-m² plots ranged from 0 to 25 seedlings m² in early June of each season with an overall average of two seedlings m². During this period, a mean of 102 ± 10 live bunchgrass culms m² accounted for 30%–40% of the surface cover, while other herbaceous species had a cover of only 5%. Approximately 50% of the space between plants was bare soil and 50% was covered with sparse *P. ponderosa* needle litter.

Summer air temperatures at 0.2 m above the soil surface had a mean daily amplitude of 15°C and mean vapor density deficits during midday of 30 g m^{-3} (fig. 1). The water potential in the upper 0.05 m of soil decreased to less than -1.5 MPa in early July, while the water potentials for soils at depths of 0.25 m and 0.5 m remained above -1.5 MPa until late July and mid-August, respectively (fig. 2A).

Pinus ponderosa seedlings developed a single taproot exceeding 0.3 m in length within 4 wk of germination. Soil water potential was greater than -0.03

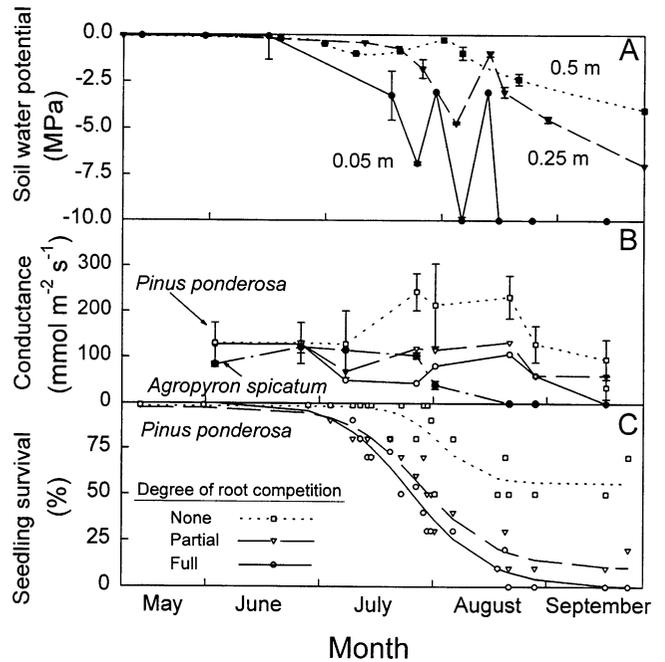


Fig. 2 A, Mean seasonal change in mean soil water potential at three different depths ($n = 6$ per point). B, Mean stomatal conductance between three pine seedling root competition treatments and established bunchgrass ($n = 20$ per point). Vertical lines on graphs A and B represent 1 standard error of the mean. C, Mean seasonal pine seedling survival for three root competition treatments ($n = 10$ seedlings per point).

MPa during this period of time. Seedling shoots that developed within 2–4 wk of germination generally had 5 ± 1 cotyledons, 33.5 ± 1.1 single juvenile needles, and a height of 0.08 ± 0.03 m. During the following 4 mo pine seedling shoots showed no significant height growth but increased from 1 to 3 mm in stem diameter. Total needle area, including cotyledons, during this period declined from $920 \pm 105 \text{ mm}^2$ to $530 \pm 75 \text{ mm}^2$ from needle senescence. A mean root: total plant biomass ratio of 0.78 ± 0.11 was observed after 4 mo.

Agropyron spicatum initiated growth in April, 1–2 mo before germination of pine seedlings, and ceased growing by the end of July. Dormancy, as evidenced by decreased stomatal conductance and increased foliage senescence, occurred during the first week in August and coincided with sharp decreases in soil water potential in the upper 0.25 m of soil (fig. 2A, B).

The fibrous root system of *A. spicatum* was concentrated in the upper 0.3 m of soil (fig. 3). The roots of *P. ponderosa* seedlings accounted for only 3% of the total root biomass in the soil volume extending 25 mm radially and 150 mm deep around each seedling. Roots of *A. spicatum* accounted for 97% of the biomass in this soil volume. Seedling mortality and stomatal conductance were significantly correlated with decreasing soil water potential (table 1). *Pinus ponderosa* seedlings exposed to full-root competition exhibited nearly 100% mortality within the first 4 mo of growth. Seedlings with roots shielded by 0.15-m- and 0.30-m-long

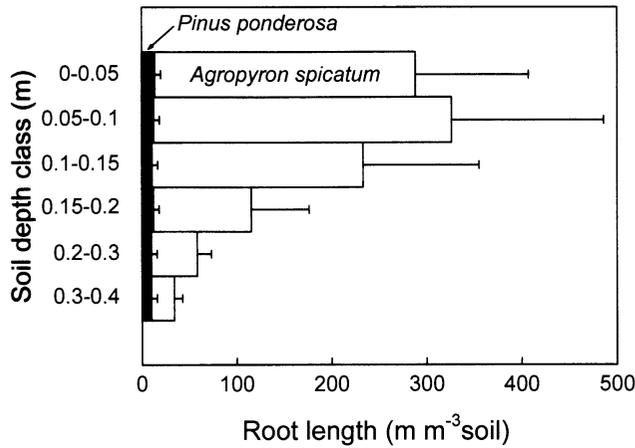


Fig. 3 Pattern of root distribution in 0.05-m depth increments for *Pinus ponderosa* seedlings and established *Agropyron spicatum* tussocks. Each bar represents the mean of 15 samples \pm 1 standard error of the mean.

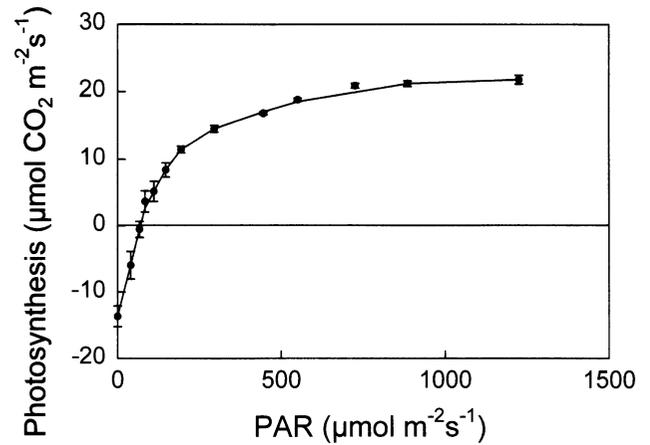


Fig. 4 Photosynthetic light response curve for *Pinus ponderosa* seedlings. Light saturation of photosynthesis occurred at approximately 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Each point represents the mean of four measurements with standard errors ranging from 2.3 to 0.20 $\mu\text{mol m}^{-2}\text{s}^{-1}$.

exclusion tubes experienced significantly delayed and lower mortality of 80% and 40%, respectively (fig. 2C). Stomatal conductance was significantly higher, by 50%, for seedlings with no root competition as compared to the other two treatments during July and August (fig. 2B).

The bunchgrass overstory around *P. ponderosa* seedlings did not significantly affect growth, stomatal conductance, or survival. Levels of PAR at solar noon indicated a nonsignificant reduction of 10% (from 2000 to 1800 $\mu\text{mol m}^{-2}\text{s}^{-1}$) in solar radiation from the *A. spicatum* canopy.

GREENHOUSE

Photosynthetic light response curves for *P. ponderosa* seedlings indicated that the compensation point for CO₂ fixation occurred at a light level of approximately 70 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and that seedlings reached light saturation at 500–600 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (fig. 4). Seedlings grown in 1-m-deep containers with three different

Table 1

CORRELATION COEFFICIENTS BETWEEN SEEDLING MORTALITY AND AMBIENT SOIL WATER POTENTIALS AT THREE DEPTHS, AND SEEDLING STOMATAL CONDUCTANCE

	Mortality of <i>Pinus ponderosa</i> seedlings with roots exposed to three levels of competition		
	Full	Partial	None
Water potential at soil depth (m):			
0.05	0.87	0.85	0.72
0.25	0.82	0.82	0.71
0.50	0.72	0.72	0.63
Stomatal conductance ($\text{mmol m}^{-2}\text{s}^{-1}$)...	0.82	0.83	0.80

Note. All showed significant correlations ($\alpha \leq 0.05$). Mortality for seedlings without root competition had the lowest correlations with measured soil water potentials.

depths of soil water recharge showed no significant differences in total biomass production after 4 mo. Root biomass and length were significantly greater in the watered container zones than the unwatered zones (fig. 5). Seedlings in all treatments developed 1.0-m-long taproots within 4 wk and maintained a root system throughout the entire container regardless of the depth of watering.

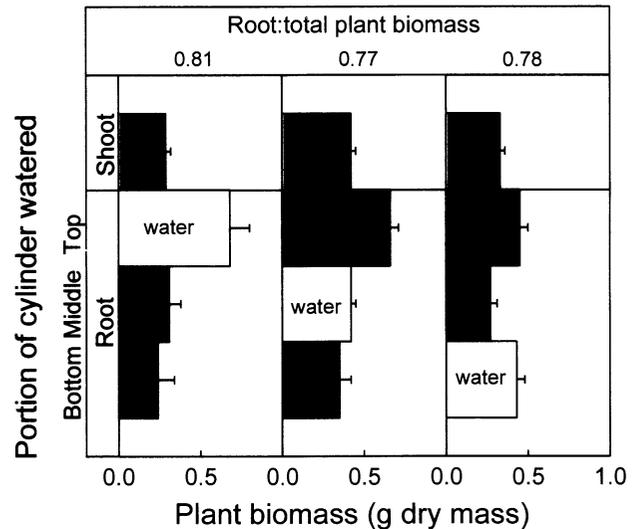


Fig. 5 Biomass distribution for *Pinus ponderosa* seedlings watered (open bar) at three soil depths in a 1-m-long cylinder. Mean total root biomass was similar for all treatments. Mean total shoot mass was significantly greater ($\alpha \leq 0.05$) only for seedlings watered at 0.3 m. Root biomass and length were significantly greater in watered soil sections than unwatered sections among treatments. The upper root biomass section for all three treatments is greater than the deeper root sections because it included the seedling root collar. Each bar represents the mean of 15 seedlings \pm 1 standard error of the mean.

Discussion

Plant species that initiate spring growth earlier than potentially competing vegetation have higher survival and productivity because of greater access to limited resources (Harris 1967; Harris and Wilson 1970; Grime 1979; Reichenberger and Pyke 1990). *Agropyron spicatum* initiated growth 1–2 mo before *Pinus ponderosa* seedlings germinated and completed its aboveground growth within the following 3 mo. *Agropyron spicatum* exhibited midsummer dormancy and regrowth after fall precipitation. Apparently, *A. spicatum* utilized water before other species became physiologically active, thereby gaining a competitive advantage in capturing this limited resource. In contrast, *P. ponderosa* seedlings appeared to rely on taproot development to utilize deeper water sources, thereby avoiding competition in the upper soil horizons where perennial bunchgrasses have the highest root density. Thus, the entire root system of pine seedlings overlaps with that of the bunchgrasses only in the spring, when soil water is still available in the upper soil horizons. This type of interspecific resource partitioning has also been described in other xeric ecosystems (Poole and Miller 1975; Wieland and Bazzaz 1975; Cody 1986; Davis and Mooney 1986; Sala et al. 1989).

Despite our observations that seedling roots extended well beyond the zone of highest bunchgrass root concentration and that the location of soil moisture had no effect on seedling growth in greenhouse tests, root overlap with *A. spicatum* in the upper 0.30 m of soil significantly increased *P. ponderosa* seedling mortality. Reductions in physiological and morphological characteristics in unshielded *P. ponderosa* seedlings were first observed when water potentials decreased in the upper soil. The water potential of ambient soil indicated that all seedlings should have been drought stressed by the first week in August. Stomatal conductance measurements, however, showed that seedlings with exclusion tubes showed no sign of drought stress until late August. Thus, as soil water was utilized, exclusion tubes provided an isolated soil volume that could be accessed only by the protected *P. ponderosa* seedlings. When the exclusion tubes were excavated at the termination of this study, soil within the tubes was moist in comparison with the dry soil surrounding the exclusion tubes. This would account for the higher stomatal conductance and survival of shielded seedlings. Exploitation of deeper soil water resources by *P. ponderosa* seedlings may also have been hindered by the lower moisture-holding capacity measured in the 0.3–0.5 soil profile compared with the upper soil layers. This would have reduced the ability of *P. ponderosa* seedlings with unshielded roots to avoid direct competition for soil water with bunchgrass roots. Thus, unshielded seedlings may have been predominantly dependent on soil water in the upper soil zones

that already had been heavily utilized by *A. spicatum* earlier in the season.

No influence of the bunchgrass overstory on *P. ponderosa* seedlings was observed in this study. Photosynthetic light response curves for seedlings acclimated to full sun in the greenhouse showed that the photosynthesis of *P. ponderosa* seedlings would not be significantly affected by a reduction in PAR of up to 70% at solar noon. Although field-grown seedlings may have had higher light saturation levels, photosynthetic rates observed for seedlings cultivated under greenhouse conditions indicate that a 10% reduction in PAR caused by a bunchgrass canopy would have little effect on carbon gain for seedlings. However, this degree of shading could have been beneficial by providing a microenvironment of cooler temperatures around seedlings and reducing respiration and evapotranspiration rates (Gates 1963). The interaction of high soil surface temperatures with drought stress may be responsible for a relatively high level of midsummer seedling mortality (Kolb and Robberecht 1996).

The *Pinus ponderosa*/*Agropyron spicatum* community appears well suited for establishment and persistence on xeric forest communities in the northwestern United States. Provided that sufficient soil depth exists for both species to exploit their respective resource pools, this community may represent a relatively stable coexistence with one species, *A. spicatum*, dominating the upper soil zone and the other, *P. ponderosa*, utilizing deeper soils. Although competition during the later stages of forest development is also important, our study focused on the interaction between newly established pine seedlings and mature bunchgrasses because the *P. ponderosa* component appears to be highly influenced by this stage in pine/bunchgrass communities. Extensive utilization and partitioning of soil resources by the species of a plant community indicate a high degree of coevolution (Parrish and Bazzaz 1976; Halpern 1988). On xeric sites with relatively shallow soils, competition for soil water between pine seedlings and established bunchgrasses may decrease the success of *P. ponderosa* seedling establishment. In environments where deeper soils are present, *P. ponderosa* seedlings can explore the soil to greater depths and eventually become dominant in a community composed of a tree overstory and an understorey of bunchgrasses (Cooper et al. 1987).

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