

Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone

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Abstract: Factors affecting the establishment of trees in subalpine meadows are important to population dynamics of trees in the alpine tree-line ecotone (ATE). Interactive effects of tree and herb cover on conifer seedlings were investigated in the ATE of the Snowy Range, Wyoming, USA. Microclimate, physiology, and survivorship of first-year conifer seedlings of *Pinus albicaulis* Engelm., *Picea engelmannii* Parry, and *Abies lasiocarpa* Hook. were measured in response to manipulations of surrounding herb and tree cover, as well as water availability. Tree and herb cover had nearly additive effects on survivorship and photosynthesis of conifer seedlings, except under alleviated water stress. In *P. albicaulis*, photosynthesis was greater near compared with away from trees and herbs, and photosynthetic efficiency (F_v/F_m) increased under herb cover. Tree cover led to greater nighttime temperatures, soil water contents, and, like herb cover, shade from solar radiation for seedlings. We did not detect any negative responses of conifer seedlings to surrounding vegetation. Furthermore, the effect of surrounding vegetation on conifer establishment appeared dependent on the type of surrounding vegetation, the species of conifer, and microsite stress level. These factors may lead to variation in the way conifer seedlings interact with surrounding vegetation and could explain changes in the relative abundances of tree species during forest succession in ATEs.

Résumé : Les facteurs responsables de l'établissement des arbres dans les prairies subalpines sont importants pour la dynamique des populations d'arbres de l'écotone alpin à la limite des arbres. Les effets interactifs des couverts herbacé et arborescent sur les semis de conifères ont été étudiés dans l'écotone alpin à la limite des arbres du Snowy Range, au Wyoming, États-Unis. Le microclimat, la physiologie et le taux de survie des semis de conifères d'un an de *Pinus albicaulis* Engelm., de *Picea engelmannii* Parry et d'*Abies lasiocarpa* Hook. ont été mesurés en fonction de manipulations des couverts arborescent et herbacé et de la disponibilité en eau. Les couverts arborescent et herbacé ont eu des effets presque additifs sur les taux de survie et de photosynthèse des semis de conifères, sauf en l'absence de stress hydrique. Dans le cas de *P. albicaulis*, le taux de photosynthèse a été supérieur à proximité des arbres et des herbacées, et l'efficacité photosynthétique (F_v/F_m) a augmenté sous un couvert herbacé. Un couvert arborescent était associé à des températures nocturnes et des teneurs en eau du sol plus élevées et, comme dans le cas d'un couvert herbacé, à moins de rayonnement solaire pour les semis. Les auteurs n'ont détecté aucune réaction négative des semis de conifères à la présence de la végétation environnante. De plus, l'effet de la végétation environnante sur l'établissement de conifères semblait dépendre du type de végétation environnante, de l'espèce de conifère et du degré de stress associé aux microsites. Ces facteurs peuvent mener à des variations dans la façon dont les semis de conifères interagissent avec la végétation environnante et pourraient expliquer les variations de l'abondance relative des espèces d'arbres au cours de la succession forestière dans les écotones alpins à la limite des arbres.

[Traduit par la Rédaction]

Introduction

Factors affecting the recruitment of trees into alpine and subalpine meadows are fundamental to tree population dynamics in alpine tree-line ecotones (ATE), transitions from forest to alpine meadow along an elevation and stress gradient. Vegetation in meadows of the ATE likely influences potential microsites for tree establishment. However, how tree

seedlings are affected by interactions with surrounding vegetation in ATEs is not well known. The highest mortality rate among life stages of tree-line conifers is in the first few years (Germino et al. 2002), thus, factors affecting survivorship of young seedlings that are 1–2 years old are crucial to tree establishment. Young seedlings of tree-line conifers tend to be much shorter (e.g., 2–5 cm in height) compared with surrounding vegetation (e.g., 10-cm grass and forbs). The ef-

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fect of overtopping, herbaceous meadow vegetation on the physiology and survivorship of young conifer seedlings is not well known for any tree-line ecotone, to our knowledge.

Positive, or facilitative, interactions among plants may increase relative to competitive effects with increasing abiotic stress (Bertness and Callaway 1994), as observed in the alpine environment (Callaway et al. 2002; Smith et al. 2003). Vegetation surrounding a plant may ameliorate harsh abiotic factors such as low growing season temperatures or solar radiation, thereby creating a more favorable microsite for plant survival and (or) growth. Conifer seedlings appeared to establish more frequently near adult trees compared with more exposed sites within the ATE (Germino and Smith 1999; Germino et al. 2002). Clumps of adult trees, referred to as tree islands, can significantly reduce solar radiation gain, thermal radiation loss, and enhance infection by mycorrhizae for seedling microsites (Ball et al. 1991; Jordan and Smith 1995; Hasselquist et al. 2005). In addition, in the dry alpine environment (Leuschner 2000; Billings 1969), water loss for seedlings may increase with distance from tree islands because of higher incident sunlight levels and wind exposure. How herbaceous vegetation affects young conifer establishment in the ATE is less clear. Germino et al. (2002) also found that seedlings overtopped by herb cover had higher survival rates than seedlings on exposed, bare soil. In contrast, Moir et al. (1999) found fewer established conifer seedlings in herbaceous vegetation in high mountain meadows, indicating that a more comprehensive analysis of the effect of herbaceous cover on conifer seedlings in the ATE is needed. Tree and herb cover are both likely to affect conifer seedling survivorship and physiology, but their relative effects on seedlings are likely to differ as a consequence of rooting depths and extent of shading. Also, how tree and herb cover interact to affect the establishment of conifer seedlings in the ATE is unknown.

Previous studies indicated that distinct successional relationships likely exist between the codominant species of Rocky Mountain tree lines. Specifically, *Pinus albicaulis* Engelm. appears to have a relatively greater ability to colonize ATE sites and initiate tree islands, whereas *Picea engelmannii* Parry and especially *Abies lasiocarpa* Hook. appear to have greater tendencies to establish under older trees, and eventually replace them (Callaway 1998; Donnegan and Rebertus 1999; Arno 2001). The specific objectives of our research were to determine (i) whether there is a net positive or negative effect of surrounding vegetation on survivorship and physiology of conifer seedlings in the ATE, (ii) whether the balance of positive and negative effects of surrounding vegetation on seedlings is modulated by direct alleviation of the biotic environment (supplemental water) or type of surrounding vegetation (herbs vs. trees), and (iii) whether species of tree-line conifers that differ in their physiology respond differently to surrounding vegetation. We hypothesized, based on successional relationships of the tree species we evaluated, that seedlings of *P. albicaulis* would exhibit a less positive response to surrounding plants than *Picea engelmannii* and especially *A. lasiocarpa*.

Materials and methods

Plot establishment

In the ATE of the Snowy Range, Wyoming, we established plots with variable cover levels of herbaceous vegetation

adult trees, for three species of first-year conifer seedlings that emerged from seeds sown in the field. We were interested in the separate and combined effects of the two types of surrounding vegetation (herbs and trees) on survivorship, physiology, and microclimate of conifer seedlings and whether the effects of surrounding vegetation changed with water availability. The supplemental water treatment was used to help identify the relative importance of above- and below-ground interactions and help expand the generality of our findings beyond the year of our study.

Site and species description

The study site was located within the alpine tree-line ecotone of the Snowy Range of the Medicine Bow National Forest in southeastern Wyoming (41°N, 106°W). The ATE of the Snowy Range is expansive and occurs over many square kilometres, spanning elevations from 3200 to 3500 m, with tree islands occurring in a patchy mosaic interspersed within alpine meadows (Oosting and Reed 1952). Our study site was at 3200 m. Cold winters typically last from September to June with minimum annual air temperatures from -25 to -40 °C. Snow depths during winter are commonly >10 m deep in the largest drifts, approximately 1–3 m deep in low wind areas, and minimal in open, wind-swept areas (Hiemstra et al. 2002). Much of the annual precipitation comes during winter as snow; snowbanks often persist into August (Oosting and Reed 1952; Billings 1969). Cumulative precipitation from October 2002 through the end of this study, in September 2003, was 899 mm, which is similar to average precipitation for these same months over the past 20 years (900 ± 17 (SD) mm/year).

The codominant conifer species in the ATE of the Snowy Range are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*A. lasiocarpa*). Whitebark pine (*P. albicaulis*) is a common species of nearby tree lines in Wyoming, Montana, and Idaho, but does not occur in the Snowy Range (Billings 1969). *Pinus albicaulis* was included to provide an interspecific gradient in physiological tolerances, ranging from low-light tolerant (*A. lasiocarpa*) to high-light tolerant species (*P. albicaulis*; Minore 1979). High mortality in *Picea engelmannii* and especially *A. lasiocarpa* limited our assessment of their physiological responses to treatments.

Experimental design

We evaluated first-year survival of seedlings that emerged from sown seeds to examine aboveground biotic factors affecting first-year survivorship. Seeds were sown on 26 June 2003 within five plots (blocks) that either had or did not have tree cover (referred to as “+tree” or “-tree”, respectively). Each plot contained a randomized, fully factorial combination of three factors: herb cover (with and without, referred to as “+herb” or “-herb”, respectively), supplemental water (with and without, referred to as “+water” and “-water”, respectively), and the three species of conifer (*Picea engelmannii*, *P. albicaulis*, and *A. lasiocarpa*), for a total of twelve 0.5-m diameter circular subplots per plot and 120 subplots total. All areas within the site had <5% slope. We sowed approximately 20 seeds of each species within each subplot, in an attempt to achieve five seedlings per subplot. Seedlings were spaced within subplots in a manner to exclude intraspecific competition, and to avoid edge effects. We staked hardware

cloth cages around subplots containing *P. albicaulis* until seeds germinated to avoid seed predators.

The hemisphere above each plot was photographed with a digital camera (Coolpix 995, Nikon USA) equipped with a fisheye lens (182°, Nikon USA) to measure differences in tree cover among blocks. From each photograph, we determined the fraction of the upper hemisphere comprising sky (%SKY). A sun path was then simulated for each photograph to calculate the minutes of sunlight per day (Gap Light Analyzer; Canham 1988). Plots with tree cover, or low %SKY, were nestled within 1–2 m on the south to southwest sides of tree islands, while plots without tree cover, or high %SKY, were located in adjacent open meadows with the nearest trees at least 20 m away.

To create –herb treatments, herbaceous vegetation was clipped to the ground surface, and cuttings were removed from the entire area of randomly selected subplots. The subplots were clipped every 2 weeks, or as needed, without disturbing soils.

The watering treatment was applied using cisterns connected to battery-operated programmable timers (model 3020 Electronic Aqua Timer, Melnor Inc., Winchester, Virginia) attached to vinyl distribution tubing. We attached 25-cm diameter loops of porous, “soaker” hose to the vinyl tubing to apply water to entire subplots. Subplots were separated by 1-m distances, and our measurements of water content did not detect any seepage of water between subplots. Timers were set to water the treated subplots for 1 h each in the morning (0600) and 1 h in the evening (2000). We validated the effect of watering on soil moisture biweekly by monitoring the volumetric soil water content (VWC, cubic metres of water per cubic metre of soil, reported as a percentage) of each subplot using a hand-held, water content reflectometer (Hydrosense, Campbell Scientific Instruments, Logan, Utah). An estimated 1 L of water was applied to each +water subplot during each watering period.

Picea engelmannii and *A. lasiocarpa* seeds were collected from adjacent high-altitude areas of Colorado (Swift Seed Co., Jaroso, Colorado), and *P. albicaulis* seeds were collected from high elevation sources in Wyoming (Coeur d’Alene Nursery, Coeur d’Alene, Idaho). Seeds were stratified before planting using the procedures identified for each species in Young and Young (1992).

Microclimate measurements

We recorded surface soil and conifer needle temperatures to compare +herb and –herb subplots within both +tree and –tree cover plots for only those subplots that also received supplemental water ($n = 3$ per treatment). Surface soil temperatures were measured from 24 June to 5 September 2003 using 24-gauge thermocouples positioned just below the soil surface (type T, copper-constantan, Omega Engineering, Stamford, Connecticut). Needle temperatures on *P. albicaulis* were measured from 1 August to 5 September 2003 using 36-gauge thermocouples carefully wrapped around cotyledons. Mean temperatures were recorded every 15 min from measurements taken at 2-min intervals using dataloggers (models 21x and 23x, Campbell Scientific Instruments). To compare the treatments, we calculated mean daily minimum, mean, and range of temperatures (ΔT ; daily mean minimum temperature – daily mean maximum).

Survivorship and physiology

Seedlings were marked after germination rates appeared to subside on 8 August and were recounted at the end of the growing season on 3 September. Survivorship was reported as a percentage of the number of individuals counted on the last sampling date, divided by the number present on the first sampling date.

Photosynthetic measurements were made at the end of the study, on 3 and 4 September 2003. We measured instantaneous photosynthetic carbon assimilation with a portable gas-exchange system (LI-6400; LI-COR Inc., Lincoln, Nebraska) equipped with a light source and CO₂ controller. Measurements were recorded at ambient CO₂ levels (370 ppm) and at a light level of 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthesis was measured on entire seedlings and was reported on a silhouette leaf area basis according to Smith et al. (1991). Leaf area was determined by digitally photographing the seedling and objects of known size (for calibration) from the angle of the LI-6400 light source and then quantified using image processing software (Image J, Scion Co., Fredrick, Maryland).

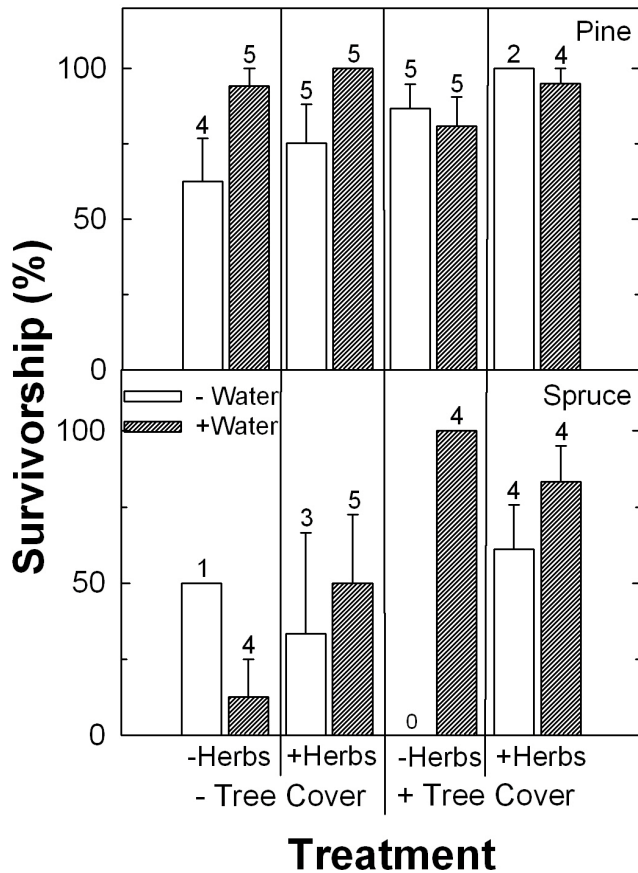
Plant water potential (Ψ_p) was measured in the field at predawn on the day following measurement of photosynthesis, immediately following harvest of seedlings, using a Scholander-type pressure bomb (model 1000, Plant Moisture Stress, Corvallis, Oregon).

Chlorophyll *a* fluorescence (MINI-PAM, Heinz Walz GmbH, Effeltrich, Germany) was also measured at predawn on the same day as Ψ_p measurements within 2 h following harvest of seedlings. Seedlings were stored in plastic bags with wet paper towels, in the dark, and on ice during this period. The ratio of variable to maximum fluorescence (F_v/F_m) was determined for dark-adapted needles by measuring the fluorescence emission from photosystem II under its completely oxidized state (F_o) and following a pulse of saturating light (F_m). From this, we determined the variable fluorescence, F_v , as $F_m - F_o$ (Krause and Weis 1991). F_v/F_m measures the maximum potential photochemical efficiency of PSII and correlates with light use efficiency measured with gas exchange (Kao and Forseth 1992). A healthy terrestrial leaf has a maximum F_v/F_m of near 0.80 (Björkman and Demmig 1987). Decreases in F_v/F_m are reflective of photoinhibition, light-dependent reductions in photosynthesis that can result from rapidly reversible and photoprotective downregulation of photochemistry, or photooxidative damage that cannot be restored, even overnight. Seedlings were then dried for 24 h at 65 °C before determining total biomass to the nearest milligram.

Statistical analyses

Significance for effects of species of seedling, tree cover, herb cover, and watering on each seedling response variable was determined using a mixed-model, split-plot ANOVA with post hoc Tukey–Kramer tests ($\alpha = 0.05$, SAS MIXED procedure; SAS Institute Inc. 2002). Because of insufficient numbers of seedlings in several treatment combinations, one-way ANOVAs were necessary to compare differences within *Picea engelmannii* and between *Picea engelmannii* and *P. albicaulis*. Differences in needle and surface soil temperatures among tree and herb cover treatments were compared using the split-plot analysis described above, with post hoc Tukey–Kramer tests ($\alpha = 0.05$). Kenward–Rogers adjustment was used to correct the denominator degrees of freedom for approximat-

Fig. 1. Mean (+1 SE) survivorship of *Pinus albicaulis* (top panel) and *Picea engelmannii* (bottom panel) seedlings among treatments. Number of replicate plots (i.e., plots with seedlings) is shown above each bar.



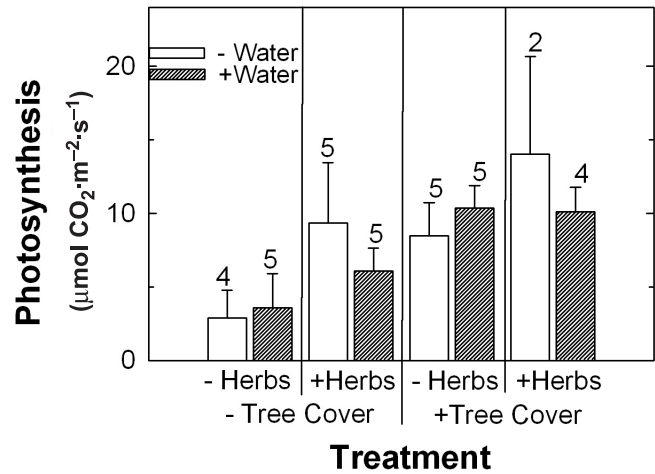
ing F distributions because of our small sample size (Schalje et al. 2002). All data were homoscedastic according to Levene's test for equality of variances ($\alpha = 0.05$), and were normally distributed according to the Shapiro-Wilk's W test ($\alpha = 0.05$).

Results

Survivorship

Few *A. lasiocarpa* seedlings germinated, and almost none lived past the first few days of emergence. Survivorship of *P. albicaulis* was 34% higher than *Picea engelmannii* in those subplots where *Picea engelmannii* was abundant enough for suitable replication (i.e., all +herb plots, $F_{[1,22.5]} = 9.39$, $P = 0.006$; Fig. 1). For *P. albicaulis* in the -water subplots, survivorship was 26% greater over all +tree compared with -tree plots, but in +water subplots, survivorship was 9.5% less over all +tree compared with -tree plots (Fig. 1, top panel; significant tree \times water interaction, $F_{[1,20.6]} = 6.5$, $P = 0.02$). In addition, there was marginal statistical support for 13% greater survival of *P. albicaulis* over all +herb compared with -herb subplots ($F_{[1,21.7]} = 3.15$, $P = 0.09$) and 15% greater survival among all +water compared with -water subplots ($F_{[1,20.6]} = 2.88$, $P = 0.105$). Among -water treatment subplots, survivorship of *P. albicaulis* increased by 17% in +herb/-tree subplots, 28% in -herb/+tree plots, and 37.5% in the combined +herb/+tree plots; compared with subplots that had no vegetation cover

Fig. 2. Differences in mean (+1 SE) photosynthesis for *Pinus albicaulis* (top panel) seedlings among treatments. Number of replicate plots is shown above each bar.



(-herb/-tree). In contrast, survivorship of *P. albicaulis* in +water subplots appeared unaffected by treatments that had vegetation, compared with -herb/-tree subplots. Survivorship of *Picea engelmannii* in water plots was about twofold greater over all +tree (81% \pm 7%) compared with -tree subplots (35% \pm 12%); a response much greater than the <10% increase observed for *P. albicaulis* (from 84% \pm 6% for -tree plots to 89% \pm 4% for +tree plots; tree \times species interaction; $F_{[1,45]} = 8.67$, $P < 0.01$; Fig. 1).

Physiological responses

Photosynthetic rates of *P. albicaulis* seedlings were about twofold greater over all +tree compared with -tree subplots (Fig. 2, top panel; $F_{[1,8.72]} = 4.37$, $P = 0.067$), and 9% greater over all +herb compared with -herb subplots ($F_{[1,21]} = 4.42$, $P = 0.048$). Photosynthesis in *P. albicaulis* responded similarly to measurements of survival among the treatments; among the -water treatment subplots, photosynthesis of *P. albicaulis* was 69% greater in +herb/-tree plots, 67% greater in -herb/+tree plots, and 79% greater in +herb/+tree plots, compared with plots that had no vegetation cover (-herb/-tree; Fig. 2). No differences in photosynthesis of *Picea engelmannii* (not shown) were detected among treatments, or compared with *P. albicaulis*, though statistical power was weak.

Mean ratios of variable to maximum fluorescence (F_v/F_m) of *P. albicaulis* increased by 6% over all +herb subplots (0.77 \pm 0.01; $F_{[1,18.4]} = 3.93$, $P = 0.06$) compared with -herb subplots (0.73 \pm 0.1; Fig. 3), regardless of watering treatment. In all other cover treatment combinations there was no statistical support or trend towards increased F_v/F_m with increased cover. Mean F_v/F_m of *Picea engelmannii* was also 7% greater over all +herb (0.72 \pm 0.02) compared with -herb (0.68 \pm 0.02) subplots, in those plots where recruitment was sufficient for replication (ie. +tree/+water subplots only, $F_{[1,6]} = 6.63$, $P = 0.049$). Over all treatments that were comparable, F_v/F_m of *Picea engelmannii* (0.71 \pm 0.01) was 7% lower than that of *P. albicaulis* (0.75 \pm 0.01, $F_{[1,46]} = 4.67$, $P = 0.036$).

Water potentials measured at predawn (Ψ_p) in *P. albicaulis* were similar across all treatments (Fig. 4). *Pinus albicaulis* had 63% greater Ψ_p (-0.22 \pm 0.08) than *Picea engelmannii*

Fig. 3. Mean (+1 SE) F_v/F_m of *Pinus albicaulis* (top panel) among treatments. Number of replicate plots is shown above each bar.

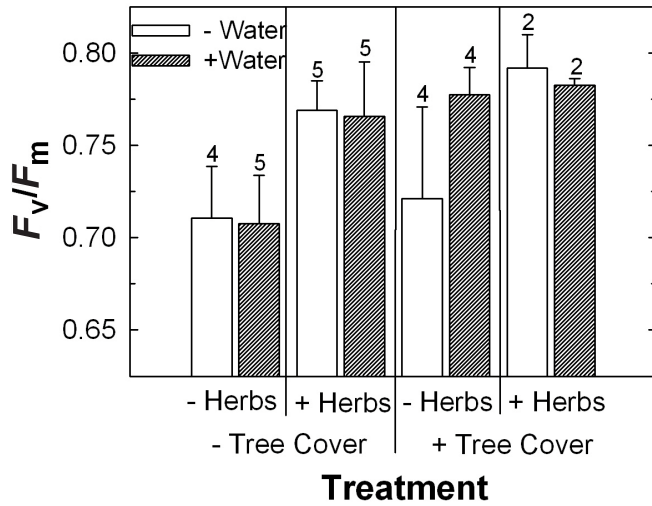
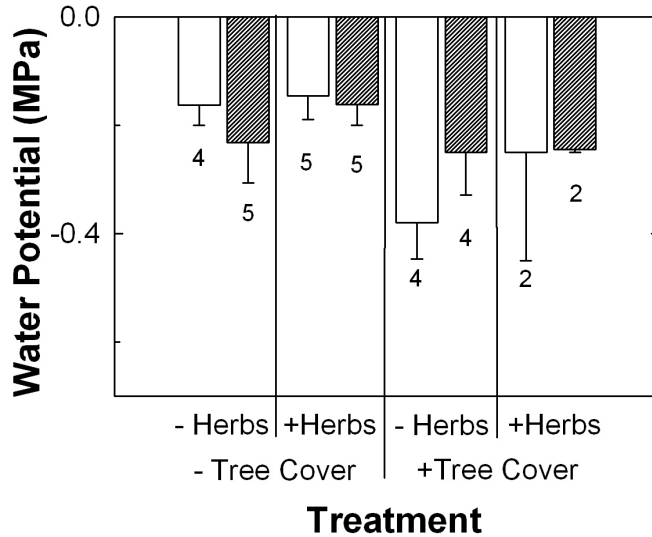


Fig. 4. Mean (-1 SE) predawn water potentials of *Pinus albicaulis* among treatments. Number of replicate plots is shown above each bar.



(-0.62 ± 0.08 , $F_{[1,46]} = 37.51$, $P < 0.001$), over all treatments that were comparable.

There were no differences in total biomass (with an overall mean biomass of 61.38 ± 4.05 mg; $F_{[1,8]} = 0.45$, $P = 0.85$) or root to shoot ratios ($F_{[1,7]} = 0.48$, $P = 0.83$) of *P. albicaulis* among the different treatments. Incomplete excavations of roots prevented a comparable analysis of biomass for *Picea engelmannii*.

Microclimate validation

Canopy cover

Plots near trees (+tree) had 22% less sky exposure (%SKY; $67.6 \pm 2.4\%$) than -tree cover plots ($86.5 \pm 0.7\%$). In addition, +tree plots had on average 21% fewer minutes of direct sunlight per day (589.1 ± 31.9 min/day) than -tree plots (749.8 ± 7.7 min/day). Herb cover ranged from 60% to nearly 100% of ground area, with canopy heights ranging

Fig. 5. Mean (+1 SE) volumetric soil water content (VWC, cubic metres of water per cubic metre of soil, reported as a percentage) among treatments. Data are based on measurements made at 2-week intervals over the growing season ($n = 15$). Bars with different letters denote significant differences at the $\alpha = 0.05$ level.

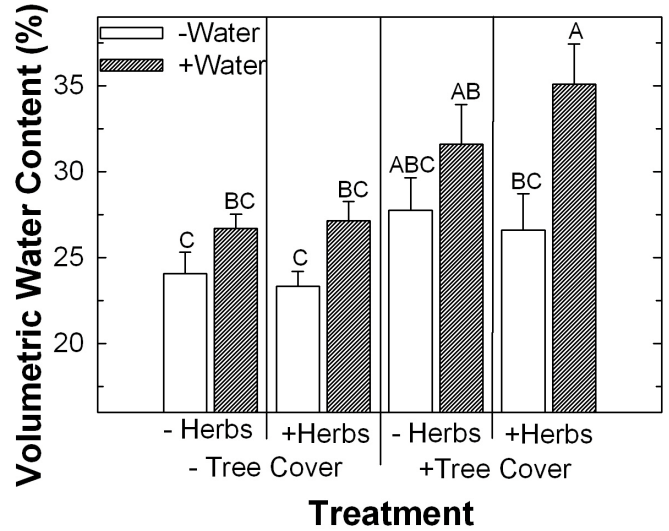


Table 1. Selected ANOVA results for microclimate validation.

Parameter	Calculation	Factor(s)	F	P	
VWC	Mean	Water	41.68	<0.001	
	Mean	Water × tree	4.17	0.044	
	Mean	Water × herb	4.06	0.047	
Temperature	Needle	Min.	Tree	4.82	0.093
		Min.	Herb	0.0	0.99
	Soil	ΔT	Tree	1.36	0.31
		ΔT	Herb	0.05	0.83

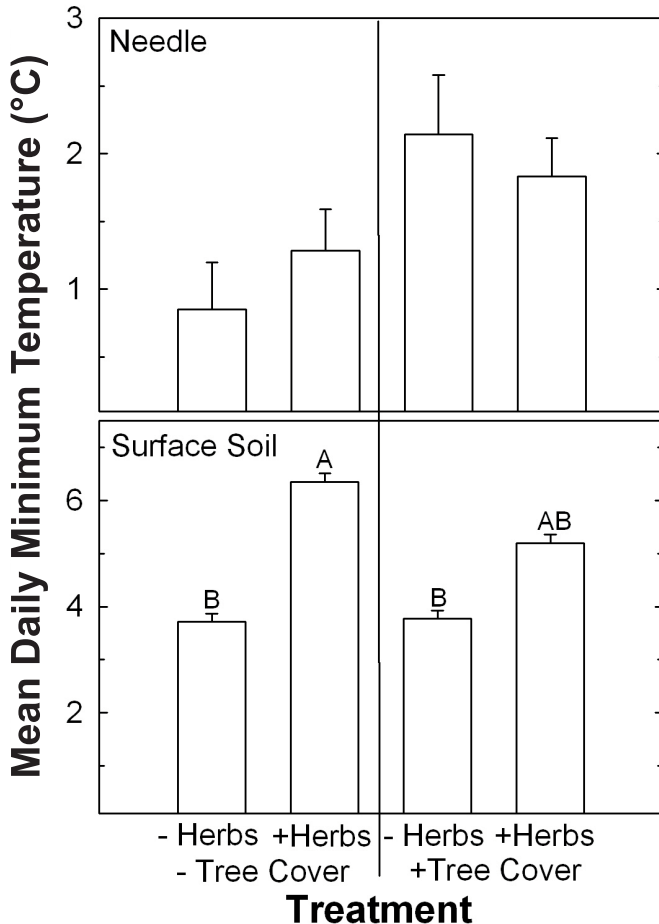
Note: All calculations are on a daily basis. Adjusted denominator degrees of freedom are 104 and 4 for volumetric soil water content (VWC) and temperatures, respectively.

from about 7 to 15 cm above ground in +herb subplots. Herbaceous vegetation appeared sparser and needle litter appeared more abundant in +tree compared with -tree plots.

Soil water content

Supplemental water (+water) and tree cover (+tree) each led to 15% higher mean volumetric water content (VWC) over all sampling dates (Fig. 5). Tree cover increased VWC less in -water subplots (13% greater VWC in +tree compared with -tree plots, $27.2\% \pm 1.4\%$ and $23.7\% \pm 0.8\%$, respectively) compared with +water subplots (19% greater VWC in +tree compared with -tree plots, $33.4\% \pm 1.7\%$ and $26.9\% \pm 0.7\%$, respectively; Table 1). Herb cover decreased VWC by 3.5% in -water subplots ($25.9\% \pm 1.2\%$ and $24.9\% \pm 1.2\%$ for -herb and +herb subplots, respectively), but increased VWC by 6% in -water subplots ($29.1\% \pm 1.3\%$ and $31.1\% \pm 1.5\%$ for -herb and +herb subplots, respectively; Table 1).

Fig. 6. Mean (± 1 SE) daily minimum temperatures for conifer needles (top panel) and surface soils of plots (bottom panel). Needle temperatures were measured from 1 August to 5 September on *Pinus albicaulis* seedlings ($n = 3$). Surface soil temperatures were measured from 24 June to 5 September ($n = 3$). Bars with different letters denote significant differences at the $\alpha = 0.05$ level.



Temperature

Mean temperatures did not differ among the treatments (Fig. 6; Table 1). However, minimum temperatures were 50% higher for needles of seedlings in +tree compared with -tree plots, and 35% higher for soil surfaces in +herb compared with -herb plots (Fig. 6; Table 1). Differences between maximum and minimum daily temperatures (ΔT) of soil surfaces were 32% lower in +herb (15.4 ± 1.1 °C) compared with -herb subplots (22.7 ± 1.5 °C; Table 1).

Discussion

Whereas previous studies asserted or inferred establishment of conifers is negatively affected by neighboring vegetation in ATEs (Körner 1998; Moir et al. 1999), we detected little evidence for competitive displacement of young conifers in the ATE. Our measurements consistently showed that conifer seedlings responded either positively or were unaffected by surrounding vegetation (see discussion on water potential below; Figs. 1–3). Moreover, we found that the effects of neighboring vegetation on conifer seedlings depended

on the type or size of surrounding vegetation, the species of conifer, and availability of water. Furthermore, herb and tree cover (i.e., +herb and +tree treatments) had nearly additive effects on survivorship under natural conditions of high stress (-water treatment), but not under less stressful conditions (+water treatment).

Separate and combined effects of tree and herb cover

Facilitation has been most frequently shown in situations where the nurse and beneficiary plants occupy a distinct canopy and subcanopy, respectively (Callaway 1995), but Choler et al. (2001) found that species of similar size may also positively influence each other. We found that trees and herbs — functional groups that either act as a distinct canopy (i.e., trees) or are similar in size and can be in nearly direct contact with seedlings (i.e., herbs) — both facilitated the survivorship and physiology of *P. albicaulis* and *Picea engelmannii* (Figs. 1–3). However, the extent of facilitation differed between the types of neighboring vegetation as well as response variables we examined. Tree cover (+tree plots) had more consistent positive effects on seedling survival than herb cover, but the benefit of herb cover was relatively more important for photosynthesis (Figs. 1–3). Positive responses of seedlings to herb cover, and especially herb and tree cover combined, highlight the importance of facilitative effects of vegetative cover for seedlings in the ATE.

Previous studies demonstrated strong positive effects of experimental shading and nocturnal warming on photosynthesis of seedlings of *Picea engelmannii* and *A. lasiocarpa* (Germino and Smith 1999), and our findings also indicate a strong role of above- compared with below-ground effects of surrounding vegetation on conifer seedlings (Figs. 2–4). The lack of increases in photosynthesis or Ψ_p in +water compared with -water subplots (Fig. 4) indicates that water was not limiting to conifer seedling photosynthesis at the time of our measurements, and that photosynthetic responses to herb and tree cover may have been mainly mediated by long-wave and solar radiation. Moreover, no Ψ_p values (Fig. 4) for seedlings near or away from neighboring plants appeared likely to elicit changes in seedling photosynthesis. Johnson et al. (2004) found that *Picea engelmannii* and *A. lasiocarpa* seedlings greater than 2 years old rarely had Ψ_p above -1.5 MPa (i.e., less negative), and photosynthesis did not respond to changes in Ψ_p above this water status. *Pinus cembra* (a stone-pine similar to *P. albicaulis*) ceases photosynthesizing at -1.5 MPa (Weaver 2001), which is considerably drier than the minimum water potential of -0.4 MPa measured for *P. albicaulis* in the current study. Despite the absence of watering effects on photosynthesis, survivorship of *P. albicaulis* was greater with supplemental water, especially when seedlings did not have the shelter of overtopping herbs and trees (Fig. 3).

Tree cover decreases solar radiation and increases long-wave radiation incident on seedling microsites, leading to warmer nights, lower ΔT values, and consequently less temperature stress for seedlings (Fig. 6; Germino and Smith 2000). We did not detect a nocturnal warming effect of herbs on conifer needles, which we suspect is due to compensating interactions of cool herb tips (from radiation loss; Ball et al. 1997) and warming of air in the boundary layer of the herb canopy by soil surfaces (which receive heat through conduc-

tion from soil depths at night; Fig. 6). Greater F_v/F_m of seedlings and lower ΔT values of surface soils in +herb compared with +tree plots indicated that herb cover may have provided more shade from solar radiation for the conifer seedlings than tree cover (Figs. 3 and 6). These changes in F_v/F_m suggest that herb cover may have prevented chronic photoinhibition by consistently shading excess solar radiation that would otherwise damage the photosystems of seedlings. Photoinhibition induced by the combination of frost and bright sunlight appeared in previous studies to cause considerable decreases in photosynthesis of conifer seedlings in exposed ATE sites (Germino and Smith 1999, 2000).

Conifer species differences

Differences in survival of seedlings of the conifer species in (*P. albicaulis* > *Picea engelmannii* > *A. lasiocarpa*) and less photoinhibition in *P. albicaulis* than in *Picea engelmannii* in the cold, bright tree-line location of this study (Figs. 1, 3, and 6) corresponded well with previous studies indicating a relatively greater ability of *P. albicaulis* to colonize sites in the ATE (Callaway 1998; Arno 2001). *Picea engelmannii* also appeared more strongly facilitated by trees than *P. albicaulis*, as indicated by a 66% greater increase in survivorship of *Picea engelmannii* in +tree compared with -tree plots, compared with *P. albicaulis* (Fig. 3). Greater adaptation of *P. albicaulis* seedlings to bright, cold, dry conditions of the ATE than *Picea engelmannii* and especially *A. lasiocarpa* may contribute to the relatively greater abundance of *P. albicaulis* in the higher, more exposed sites of ATEs (Arno 2001). Similarly, Callaway (1998) found *P. albicaulis* had older establishment dates than *A. lasiocarpa* located within the same tree islands at tree line, indicating possible facilitation of *A. lasiocarpa* establishment by *P. albicaulis*. Moreover, *A. lasiocarpa* had higher growth rates in microsites closer to *P. albicaulis*, at high elevation sites (Callaway 1998). Our findings suggest that even though *P. albicaulis* has a relatively greater colonizing ability than the other species, its establishment can still be enhanced by both herb and tree cover. Similarly, 81% of the regeneration microsites for *P. albicaulis* were within 15 cm of trees, rocks, vegetation, and other objects in forest that were at much lower elevation than in the current study (Tomback et al. 1993). Seedlings of *A. lasiocarpa* showed greater reductions in photosynthesis in response to frost and bright sunlight than seedlings of *Picea engelmannii*, in a previous field study at tree line (Germino and Smith 1999). These results indicated greater susceptibility to low-temperature photoinhibition in *A. lasiocarpa* compared with *Picea engelmannii*, which corresponded with relatively lower abundances of *A. lasiocarpa* than *Picea engelmannii* in the ATE (Germino et al. 2002) and relatively higher recruitment of *P. engelmannii* into ATE plots in the current study. These interspecific differences in physiology of *A. lasiocarpa* and *Picea engelmannii*, as well as the differences between *P. albicaulis* and *Picea engelmannii* in the current study, indicate that physiological differences in response of seedlings to low temperatures and bright sunlight may contribute to successional relationships among conifer species in the ATE. Moreover, unique physiological properties of dominant tree-line species may strongly affect the rate and pattern of tree recruitment as climate changes (Dullinger et al. 2004).

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