ÉCOSCIENCE
13 (3): 334-341 (2006)

Microsite differentiation among conifer species during seedling establishment at alpine treeline[1]

Eliza L. MAHER[2] & Matthew J. GERMINO[3], P.O. Box 8007, Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007, USA, e-mail: germmatt@isu.edu

Abstract: Tree establishment is a potentially important factor affecting tree populations in alpine-treeline ecotones. Patterns of seedling establishment of *Abies lasiocarpa*, *Pinus albicaulis*, and *Picea engelmannii* were evaluated relative to neighbouring trees and herbs over two years and three treelines of the Rocky Mountains, USA. The greatest mortality rates were observed in seedlings that had just emerged from seed and were in their first year of growth and in seedlings that had the least amount of cover provided by trees or other landscape features that block exposure to the sky. Although herb cover promoted survivorship in microsites that were not near trees, no seedlings were detected at or above the upper limit of the treeline ecotone. Microsite tree cover was greatest for *A. lasiocarpa* and least for *P. albicaulis* seedlings, which matches predictions based on their relative photosynthetic tolerances to the bright sunlight and frequent frost that occur in exposed microsites. Interspecific differences in seedling requirements for neighbouring plant cover likely contribute to the apparent coexistence and possible interdependency of these conifers along a continuum of colonization and succession within treelines.

Keywords: *Abies lasiocarpa,* alpine treeline, *Picea engelmannii, Pinus albicaulis,* seedling establishment.

Résumé : L'établissement est un facteur potentiellement important affectant les populations d'arbres dans les écotones de la limite alpine des arbres. Les patrons d'établissement de *Abies lasiocarpa*, *Pinus albicaulis* et *Picea engelmannii* ont été étudié en relation avec la couverture d'arbres et d'herbes voisins, sur une période de deux ans dans trois secteurs à la limite des arbres dans les montagnes Rocheuses des États-Unis. Les taux les plus élevés de mortalité ont été observés pour les semis qui venaient tout juste d'émerger de graines et qui étaient dans leur première année de croissance et pour ceux qui avaient la moins grande couverture d'arbres ou d'autres éléments du paysage leur masquant le ciel. Même si la couverture herbacée favorisait la survie dans les microsites éloignés d'arbres, aucun semis n'a été détecté à la limite supérieure de l'écotone forestier ou au-dessus de celle-ci. La couverture d'arbres des microsites était la plus élevée pour *A. lasiocarpa* et la moins élevée pour *P. albicaulis,* ce qui concorde avec les prédictions basées sur leur tolérance photosynthétique relative au rayonnement intense et au fréquents gels qui affectent les microsites exposés. Des différences interspécifiques dans les exigences des semis au niveau de la couverture de plantes voisines contribuent probablement à la coexistence et la possible interdépendance des conifères le long d'un continuum de colonisation et de succession à la limite des arbres.

Mots-clés : *Abies lasiocarpa*, établissement de semis, limite alpine des arbres, *Picea engelmannii*, *Pinus albicaulis*.

Nomenclature: Hitchcock *et al.*, 1969.

Introduction

Factors affecting the abundance of trees are important for understanding alpine-treeline ecotones (ATEs), the transition zones between forest and alpine communities. Physiological factors affecting tree growth are well known to limit forest development in ATEs (Hadley & Smith, 1986; Körner, 1998). However, the role of recruitment limitations and biological factors affecting tree recruitment in ATEs has not received as much attention, particularly compared to savanna and other situations where trees coexist with herbaceous species (*e.g.,* reviewed in Sankaran, Ratnam & Hanan, 2004).

In ATEs, trees are often clustered in islands that are interspersed by herb-dominated, subalpine meadows, particularly in sites that are not unusually steep or substrate-limited (Billings, 1969). Thus, trees in ATEs are likely to have significant interactions with herbaceous species as well as other tree species. Seedling responses to neighbouring vegetation are an important aspect of regeneration niches and the corresponding structure of forests, particularly in the context of disturbance–succession cycles (Grubb, 1977; Knapp & Smith, 1982; Aplet, Laven & Smith, 1988; Donnegan & Rebertus, 1999). In harsher environments such as ATEs, plants such as tree seedlings are predicted to respond positively to neighbouring vegetation (Callaway, 1998; Germino, Smith & Resor, 2002), though some studies indicate possible negative responses of tree seedlings to neighbouring plants in ATEs (Körner, 1998; Moir, Rochelle & Schoettle, 1999). Moreover, tree species that co-dominate ATEs can differ in their responses to high-elevation stresses (Germino & Smith, 1999; Handa, Körner & Hättenschwiler, 2005), which could promote interspecific variation in seedling responses to neighbourhood plants and regeneration niche. Variation in regeneration niche could, in turn, contribute to coexistence of tree species in the context of tree colonization and seral replacement in subalpine meadows (Connell & Slatyer, 1977; Bazzaz, 1979).

---

[1] Rec. 2005-06-13; acc. 2005-11-28.
Associate Editor: Håkan Rydin.

[2] Present address: Center for Natural Lands Management, Fallbrook, California 92028, USA.

[3] Author for correspondence.

Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) are frequent, co-dominant species of high-elevation forest in the Rocky Mountains (Oosting & Reed, 1952). Interspecific differences in age and radial growth suggest that *P. albicaulis* may initiate tree island formation by colonizing ATE meadows and then facilitating growth of neighbouring *A. lasiocarpa* (Callaway, 1998). Trees as well as herb cover can influence wind, snow deposition, water availability, mycorrhizal inocula, and other soil properties of potential microsites for tree seedlings (Billings, 1969; Hättenschwiler & Smith, 1999; Seastedt & Adams, 2001; Hasselquist *et al.,* 2005; Germino *et al.,* 2006). Responses of conifer seedlings to manipulations of neighbouring plant cover and microclimate revealed that protection from bright sunlight and temperature extremes are also particularly important ways that trees facilitate growth and survival of newly germinated seedlings in ATEs (Germino & Smith, 1999; 2000). Tree cover led to greater photosynthesis and survivorship of emergent conifer seedlings in an ATE, especially in *A. lasiocarpa* compared to *P. albicaulis* or *P. engelmannii* (Maher, Germino & Hasselquist, 2005). Interspecific differences in photosynthetic tolerances to light and temperature could affect seedling growth and stress tolerance, and lead to species differences in seedling requirements for neighbouring plant cover in ATEs.

Our objectives were to determine (1) how neighbouring tree and herb cover influences regeneration niches of *P. albicaulis*, *P. engelmannii*, and *A. lasiocarpa* in ATEs and (2) whether interspecific differences in seedling requirements for cover could contribute to greater ecological relationships of these conifers in ATEs. We observed where seedlings of each conifer species emerged, initially survived, and appeared to establish relative to neighbouring herb and tree cover within three ATEs of the Rocky Mountains. We hypothesized that the youngest conifers would survive more frequently near herbs and especially trees, reflecting microsite selection for shelter from harsh sunlight and temperatures. Whereas herbs and trees can shelter young conifers from severe climate in the ATE, herbs are also more likely to share root zones and compete with seedlings for soil resources. We therefore hypothesized that seedlings would have more positive responses to trees than to herbs. Furthermore, we predicted that *A. lasiocarpa* would exhibit the greatest selection for microsite cover, whereas *P. albicaulis* would occur in microsites farthest from neighbouring plants, based on their photosynthetic tolerances to temperature and sunlight. Lastly, we hypothesized that variation in the relative abundances of the tree species would correspond with differences in advance tree establishment among ATEs, due to interspecific differences in seedling requirements for tree cover.

Methods

SITE AND SPECIES DESCRIPTIONS

Study sites were located within the alpine-treeline ecotones of the Beartooth Mountains of the Shoshone National Forest (45° N, 109° W), the Teton Mountains of the Targhee National Forest (43° N, 110° W), and the Snowy Range Mountains of the Medicine Bow National Forest (41° N, 106° W), all in Wyoming, USA. Treeline elevations were approximately 2950 m in the Beartooths, 2900 m in the Tetons, and 3200 m in the Snowy Range. In all mountain ranges, approximately 80% of the annual precipitation (about 1 m) comes during winter as snow, and snow banks often persist into July (Oosting & Reed, 1952; NRCS, SNOTEL data network).

In the Snowy Range, *P. engelmannii* and *A. lasiocarpa* are co-dominant ATE species, whereas ATEs of the Beartooth and Teton study areas had these species and *P. albicaulis*. Johnson and Billings (1962) broadly define the alpine herbaceous communities in the Beartooths as dominated by *Geum rossii* turf on summits, ridges, and upper slopes, while *Deschampsia cespitosa* meadows occurred on moist to mesic slopes and depressions. Billings and Bliss (1959) described the herbaceous community of alpine meadows in the Snowy Range as dominated by *Salix cascadensis*, *Geum tubinatum*, *Trifolium parryi*, *Artemisia scopulorum*, and *Carex drummondiana*. Herbaceous communities in the Beartooths and Snowy Range were typically near 10 cm in height above ground. Herbaceous meadow vegetation in the Tetons appeared dominated by *Epilobium latifolium*, *Lupinus* spp., *Aster* spp., and *Daucus* spp. (Spence & Shaw, 1981). Heights of meadow communities in the Tetons often reached 50 cm, but were typically near 25 cm above ground.

SURVEYS OF YOUNG CONIFERS

We measured emergence and survivorship of young conifers in eight 0.09-ha plots using a stratified random sampling scheme in each of the three mountain ranges. Sampling occurred during the growing seasons of 2002 and 2003. Plots were positioned to ensure that microsites with a wide range of tree cover were consistently evaluated in each mountain range. We established three plots in the uppermost limits of closed-canopy forest, three plots in ATE meadows having tree islands (timberline), and two plots in open alpine meadows (just above treeline). Plots were located in sites that appeared representative of each life zone, were relatively level, and did not have unwanted features such as excess rock and minimal soil substrate for seedling microsites. In each plot, we established one 30-m baseline with eight 30-m transects perpendicular to the baseline at 3.75-m intervals starting at 0 m. Along each transect, we recorded the presence of young conifers in nine randomly placed 0.5-m^2 quadrats and marked conifers in the quadrats to monitor their survivorship. We monitored a total of 72 quadrats (36 m^2) per 0.09-ha plot, for a total of 576 quadrats (288 m^2) per mountain range, for newly emerged conifers and for survivorship of previously marked young conifers monthly throughout the growing seasons of the 2-y study. We categorized conifers as "first-year emergent" (less than 1 y old, with cotyledons), "seedling" (an individual that still had cotyledons but was not a first-year emergent), and "juvenile" (an individual under 30 cm tall). First-year emergents, seedlings, and most juveniles were under 5 cm in height. We marked 239 young conifers for monitoring in 2002. In 2003, a flush of emergent seedlings in the Snowy Range increased the number of young conifers monitored to 763.

Two different approaches were needed to assess the tree cover above and herbaceous cover around young conifers.

Tree cover above each young conifer was photographed with a digital camera (Coolpix 995, Nikon USA, Melville, New York, USA) equipped with a fisheye lens (182°, Nikon USA) in order to measure the extent of interaction among adults and young conifers. From each photograph, we determined "sky exposure" (%SKY), which is the percent of the upper hemisphere above a microsite composed of sky compared to sky-occluding features such as tree branches. %SKY was determined with Gap Light Analyzer software (Canham, 1988). Lower %SKY values generally indicated more tree cover, except in the Tetons, where herb cover was over 20 cm in height, the height of the camera and lens combined. Additionally, to characterize the range of %SKYs available to seedlings within a plot, we took three hemispherical photographs at randomly selected points along each transect for a total of 24 site photographs per plot and 192 site photographs per mountain range.

Herbaceous vegetation surrounding each young conifer was quantified by photographing the ground area (0.5 m^2) from 1 m height. The density of herbaceous vegetation was visually estimated from photographs and categorized into one of four nominal levels: 1) no herbs within 10 cm of young conifers; 2) sparse herbs within 10 cm, but not shading the conifer; 3) herbs within 10 cm and appearing capable of shading the conifer; and 4) dense herbs (approximately 70% cover) within 10 cm, appearing able to shade the conifer.

Survivorship of young conifers was reported as the number of individuals in a plot counted on the last sampling date divided by the number of individuals present in a plot on the first sampling date.

STATISTICAL ANALYSES

We used univariate two-factor analysis of variance (ANOVA) to determine differences in the abundances of each conifer species among mountain ranges, based on counts from our initial survey in 2002. Single-factor ANOVA was used to compare survivorship among the life stages within each species of conifer and to compare survivorship of first-year emergents among species. Plots ($n = 8$ per mountain range) were the unit of replication for analyses of abundance and survivorship of conifers. Tukey–Kramer tests were used to detect differences among different combinations of factors (SAS Institute, 1999).

The nonparametric Kuiper's test was used to assess differences in dispersion, or range, of %SKYs among (1) microsites available to seedlings within plots (a random sample of microsites within plots), (2) first-year emergents, and (3) older seedlings within each mountain range. This allowed us to determine if young conifers were selectively establishing in lower or higher %SKYs (closer to or farther away from tree cover) than %SKY among microsites available to them. Analyses were conducted for all species separate and combined, to determine differences among species and mountain ranges. The Kuiper's test is closely related to the more well-known Kolmogorov–Smirnov test (or K–S test), but Kuiper's test is as sensitive to differences in the tails as in the medians of distributions (Zar, 1999). Kuiper's test was also used to compare the range of densities of herbaceous cover for first-year emergents and older seedlings within mountain ranges. All analyses using Kuiper's test were based on individual photographs from either random samples or conifers pooled from plots within each mountain range. When describing differences using Kuiper's test, we reported medians as well as quartile ranges (difference between the 25th and 75th percentile values).

Finally, we calculated log-likelihood ratios (χ^2 from *G*-test; Zar, 1999) in a contingency table to determine if the ratio of the number of alive compared to dead individuals in our final sampling was affected by whether the seedling had no vegetative cover, herb cover, tree cover, or both herb and tree cover. For this analysis, young conifers with herb cover values of "1" and "2" were grouped into a low herb cover category (- herb) and young conifers with herb cover values of "3" and "4" were combined into a high herb cover category (+ herb). Similarly, young conifers with%SKY values greater or less than 40% were assigned to low and high tree cover categories (- tree and + tree), respectively. For example, a seedling with 30% SKY and a nominal herb cover value of "1" was coded as having low herb and high tree cover.

Results

GENERAL PATTERNS OF ABUNDANCE AND SURVIVAL

Young conifers were not found in the alpine plots of any mountain range, so results are based on conifers detected in the forest and treeline. Abundances of emergents, seedlings, and juveniles combined for each conifer species differed among mountain ranges, with no *P. albicaulis* detected in the Snowy Range, few *P. engelmannii* in the Tetons, and few *A. lasiocarpa* in the Beartooths (Figure 1; $F_{4, 53} = 3.91$, $P < 0.001$).

No differences in survivorship were detected among mountain ranges and years within each species (not shown); we therefore combined these factors for analysis of survivorship. Mean survivorship of first-year emergents was 84% lower than for older seedlings or juveniles in *A. lasiocarpa* (Figure 2; 0.15 ± 0.06%, mean ± SE; $F_{2, 25} = 91.04$, $P < 0.001$) and *P. engelmannii* (0.071 ± 0.071%, mean ± SE; $F_{2, 17} = 7.54$, $P < 0.01$). No differences were found in survivorship between seedlings and juveniles; hence, these life stages were grouped into "older seedlings" for the remainder of our analyses. Mean survivorship of first-year emergents was three-fold greater in *P. albicaulis* than in *A. lasiocarpa* or *P. engelmannii* (Figure 2; $F_{2, 21} = 7.83$, $P = 0.003$; Tukey–Kramer). The number of emergents was similar between 2002 and 2003 in the Beartooths and Tetons, but ranged from zero in 2002 to 400 in 2003 in the Snowy Range. Most mortality was observed in summer, and only three young conifers died over the winter of 2002–2003. We observed the dead conifer (*e.g.,* individual with all needles brown and shrivelled) for > 95% of the mortality events recorded, and we otherwise detected no losses due to predation, herbivory, or disease.

SKY EXPOSURE AND TREE COVER

First-year emergents occurred in microsites closer to trees (in low %SKY) and in smaller ranges of %SKY compared to the %SKY of microsites available to them in sample plots in the Beartooths and Tetons but not in the

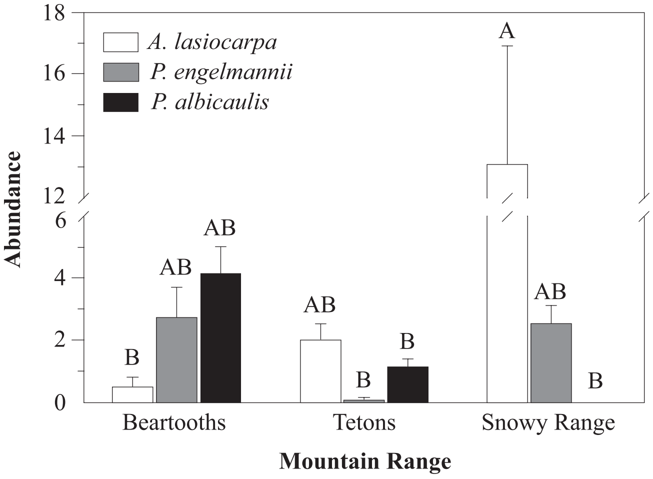

FIGURE 1. Abundance of *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus albicaulis*, within the Beartooths, Snowy Range, and Tetons. Data are mean number of emergents, seedlings, and juveniles combined per 36-m^2 plot + 1 SE. Letters above bars denote significant differences at $\alpha = 0.05$ using two factor ANOVA followed by *post hoc* Tukey–Kramer tests. Seedlings were only found in ATE and forest plots; therefore, $n = 6$ plots per species, per mountain range.

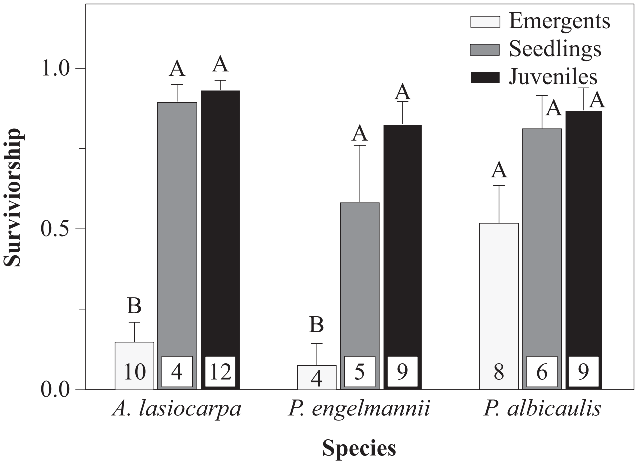

FIGURE 2. Differences in survivorship (mean fraction of individuals surviving + 1 SE) for the different life stages of *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus albicaulis* over all mountain ranges combined. Different letters represent significant differences among life stages within each species at $\alpha = 0.05$ as determined by single factor ANOVA followed by *post hoc* Tukey–Kramer tests. Numbers of replicate plots are shown in each bar.

Snowy Range, as illustrated by comparisons of median and range of quartile values of %SKY for plots and emergents in Figure 3. Older seedlings were found in microsites even closer to trees (in lower %SKY) and in smaller ranges of %SKY compared to emergents, overall sites, and species. The ranges of quartile values of %SKY for older seedlings were 35–80% smaller than for all microsites available to seedlings within sampling plots, and median %SKY was 24–41% less for older seedlings than available microsites (Figure 3). Median values and ranges of %SKY were several-fold smaller for older seedlings compared to emergents in the Beartooths and Snowy Range, but not in the Tetons (Figure 3). Median and mean %SKY for older seedlings, over all species, was 60% greater in the Beartooths and Tetons than in the Snowy Range (df = 137 and 173, $K_a = 3.33$ and 3.81, and $P < 0.0001$, for pairwise comparisons of Tetons or Beartooths to Snowy Range, respectively).

HERBACEOUS COVER

In the Beartooths, median and mean herb cover was greater for older seedlings than for emergents, but ranges of cover were similar among the ages (Table I). There was no statistical support for greater herb cover for older seedlings compared to emergents in the Tetons. Emergents in the Snowy Range had amounts of herb cover similar to that of older seedlings, but older seedlings occurred in a much narrower range of herb cover than emergents (Table I). No differences in herb cover were detected among species over all mountain ranges or life stages combined. Mean ± SE herb cover values over all species and mountain ranges were 2.1 ± 0.05 for emergents and 2.4 ± 0.06 for older seedlings, but median values were 2 for each life stage. Lower and upper quartile values were 1 and 3 for emergents and 2 and 3 for seedlings, respectively, over all species and mountain ranges.

INTERACTIVE EFFECTS OF TREE AND HERBACEOUS COVER

The ratio of the number of individuals that were still alive at the last sampling compared to number of seedlings that died (alive:dead) in microsites without tree cover (in high %SKY) was higher when conifers had high herb cover compared to when conifers had low herb cover for all species, developmental stages, and mountain ranges combined (Figure 4; $\chi^2 = 16.92$, $P < 0.001$). In contrast, the ratio of alive:dead seedlings in low %SKY near trees was not affected by herb cover ($\chi^2 = 0.08$, $P > 0.05$).

DIFFERENCES IN SKY EXPOSURE AMONG SPECIES

The range of microsite %SKY in which first-year emergents were detected differed among the tree species (Figure 5, top panel; Table II). Median values of %SKY for emergents appeared similar among the species, though emergents of *A. lasiocarpa* occurred in a 13–35% wider range of microsites than *P. engelmannii* or *P. albicaulis*. In contrast, older seedlings of *A. lasiocarpa* occurred in microsites closer to trees, with up to a 35% lower and a ~50% narrower range of %SKY than either *P. engelmannii* or *P. albicaulis* (Figure 5, lower panel; Table II).

Discussion

Cover provided by neighbouring plants appeared to be a positive factor defining the regeneration niche of the > 700 conifers we evaluated over 2 y in three ATEs. Young conifers were absent at or above the upper limit of treeline but were found in microsites with relatively low %SKY, close to adult trees in lower elevations in the ATEs (Figure 3). When young conifers were not located near adult trees (in high %SKY), herbaceous cover greatly enhanced their survival (Figure 4). Correlations established in the current study indicate—but do not confirm—direct effects of neighbouring plants on survival of conifer seedlings in ATEs. However, the positive relationships of conifer seedlings and neighbouring plants reported here are consistent with previous studies of conifer seedling responses to experimental manipulations of neighbouring plant cover in the Snowy Range ATE (Maher, Germino & Hasselquist, 2005).

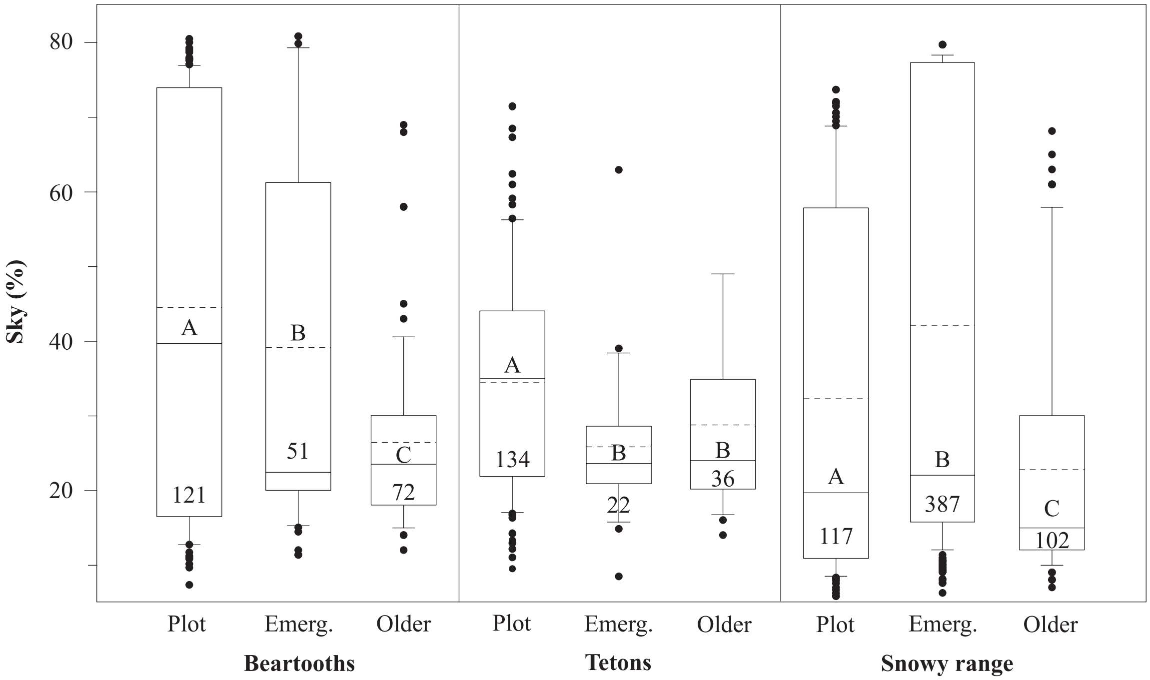

FIGURE 3. Sky exposures (%SKY) available within plots (Plot) and %SKY of microsites occupied by emergent (Emerg.) or seedlings and juveniles (Older) of *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus albicaulis* over all mountain ranges combined. The boundaries of boxes indicate the 25th and 75th percentile values (quartiles), the solid line within the box marks the median, and the dotted line indicates the mean. Whiskers above and below the box indicate the 90th and 10th percentiles, respectively; outlying points are also graphed. Different letters above the median lines denote significant differences among plots, emergents, and seedlings within each mountain range at $\alpha = 0.05$ as determined by the nonparametric Kuiper's test. Numbers of replicates are shown in each bar.

TABLE I. Nominal values of herb cover (median; quartile range followed by mean ± SE) and Kuiper's test statistics, df, and significance level for comparisons of distributions of herb cover among microsites occupied by emergents or older seedlings in each mountain range. Quartile range is the difference between the 25th and 75th percentile values. ** for $P < 0.01$ and *** for $P < 0.001$.

		Herb cover	
	K_a (df)	Emergent	Older
Beartooths	2.59 (90)***	1; 1 1.7 ± 0.2	2.5; 1 2.5 ± 0.1
Tetons	0.63 (52)	2; 1 2.2 ± 0.2	3; 1 2.7 ± 0.1
Snowy Range	2.18 (436)**	2; 2 2.0 ± 0.0	2; 0 2.2 ± 0.1

SIGNIFICANCE OF EMERGENT LIFE STAGE

Although our study did not evaluate seed deposition, germination, or growth and survival of older life stages on microsite patterns of trees, our findings for seedlings can be related to previous studies to generate insight on relative effects of different life stages on tree establishment patterns in ATEs. Greater establishment near existing trees is likely enhanced by greater seedling survival, but might also be promoted by greater seed deposition or germination (Tranquillini, 1979). For example, caching of *Pinus albicaulis* seeds by Clark's nutcracker (*Nucifraga columbiana*) is more common near trees than in open terrain (Tomback, 1978), but *P. albicaulis* established in the greatest %SKY of all species (Figure 5). Further support for the relative importance of selective survival of emergent seedlings in determining establishment patterns (Figure 4) comes from (1) seedling emergence in a wider range of microsites than those where seedlings ultimately survived and established (Figures 3 and 5), (2) low mortality rates after the first year of growth (Figure 2), and (3) little variation in microsite cover among older seedlings and juveniles. The conifers we evaluated are likely culled within months of germinating from microsites that are not sheltered by neighbouring plants.

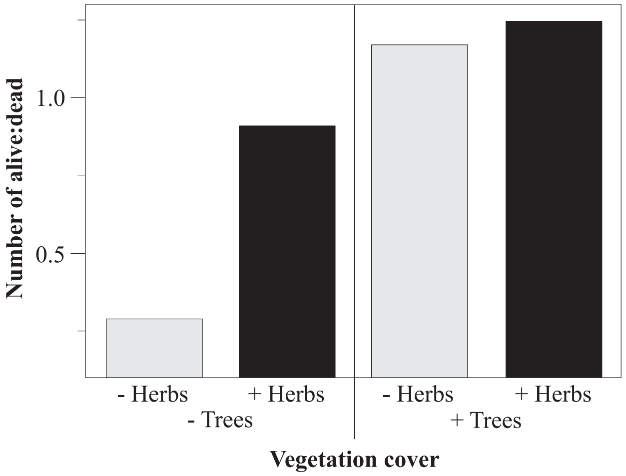

FIGURE 4. Ratio of the number of alive:dead conifers at the end of the study in response to different levels of surrounding herb and tree cover, for all species, developmental stages, and mountain ranges combined. "+ herb" and "- herb" designate conifers with nominal herb values of 3–4 and 1–2, respectively, and "- tree" and "+ tree" designate conifers with %SKY values greater and less than 40%, respectively. Data are for $n = 671$.

The long-lived nature of most conifers likely minimizes the effect of adult survivorship on population dynamics. However, slightly greater lifespans are expected for

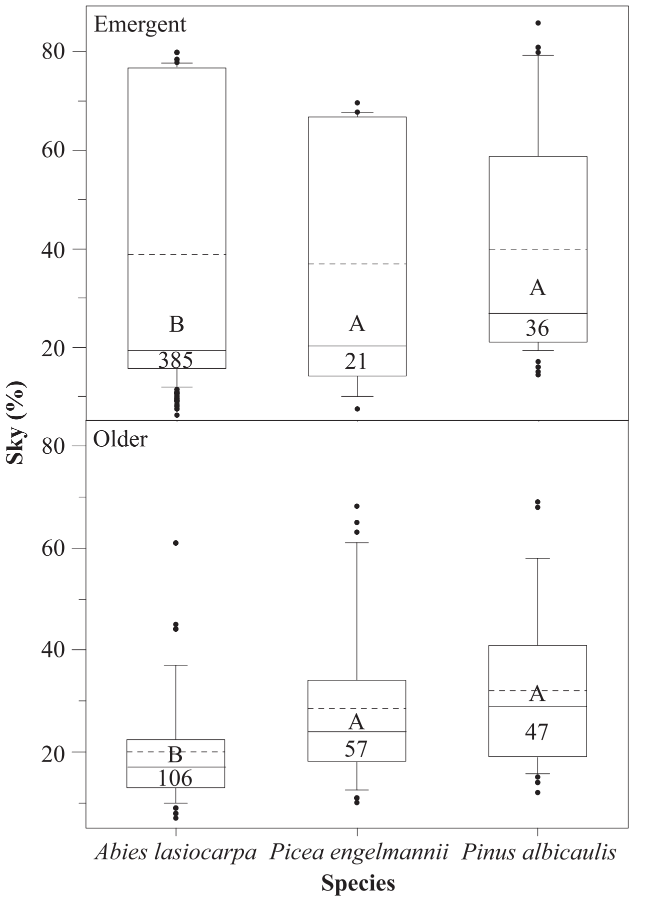

FIGURE 5. Range of sky exposures occupied by emergent (top panel) or older (seedlings and juveniles; bottom panel) individuals of *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus albicaulis* over all mountain ranges combined. Conventions of box and whisker plots are described in Figure 3. Different letters represent significant differences among species at $\alpha = 0.05$ as determined by the nonparametric Kuiper's test (Table II). Numbers of replicates are shown in each bar.

P. engelmannii than *A. lasiocarpa* (Veblen, 1986), and higher incidences of adult mortality occur in *P. albicaulis* due to disease (white pine blister rust; reviewed in Tomback, Arno & Keane, 2001). We observed no mortality in older trees in our plots during our study years (M. J. Germino, pers. observ.). Relatively less mortality in established trees compared to emergent seedlings would seem to indicate less opportunity for spatial patterning following establishment. We are not aware of any reports on microsite patterns of tree mortality, but landscape variation in height growth of trees is likely. Following establishment, height growth of conifers can be inhibited by wind-driven losses of biomass during winter and temperature effects on growth during growing seasons (Hadley & Smith, 1988; Handa, Körner & Hättenschwiler, 2005). Wind and microclimate factors affecting height growth of trees are heterogeneously applied to ATE landscapes due to topography and other factors. Smith *et al.* (2003) proposed that clustering of upright trees (high number of trees/area) in tree islands also ameliorates wind and microclimate conditions for individual tree trunks, thereby promoting their height growth. These considerations point to an important feedback in the growth of ATE tree populations in which tall trees promote seedling establishment, but seedling establishment is required to promote sufficient stem densities for height growth of trees.

TABLE II. Kuiper's test statistics, df, and significance level for comparisons of distributions of sky exposure (%SKY) among species within emergent or older seedling age classes. * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$.

	Age class	
	Emergent	Older
A. lasiocarpa versus P. engelmannii	2.20 (406)**	2.34 (162)***
A. lasiocarpa versus P. albicaulis	3.40 (420)***	2.73 (152)***
P. engelmannii versus P. albicaulis	1.61 (160)	1.49 (69)

EXPLANATIONS FOR COVER EFFECTS ON SEEDLING SURVIVAL

A number of microsite factors could change with increasing tree cover or lower %SKYs, such as snowdrift formation (Billings, 1969), colonization by symbiotic fungi and corresponding benefits for soil resource uptake (Hasselquist *et al.,* 2005; Germino *et al.,* 2006), soil nutrients or organic content (Van Miegroet, Hysell & Johnson, 2000; Seastedt & Adams, 2001), or water availability. We found little evidence that winter conditions could affect seedling survival patterns, and the high over-winter survival of seedlings may relate to their small height and the likelihood of snow coverage that provides protection from wind and other stresses during winter (Hadley & Smith, 1988). Others found that *P. engelmannii* and *A. lasiocarpa* seedlings were unresponsive to nutrient enrichment but were affected by variation in light and temperature (Lajzerowicz *et al.,* 2004), and Maher, Germino, and Hasselquist (2005) found that water status of *P. albicaulis* was not responsive to manipulations of herbs or distance to trees. Tree or grass cover might also affect predation, herbivory, or disease of seedlings, but we observed little evidence for these agents, either above- or below-ground, among the > 2000 naturally occurring young conifers monitored here and in our previous studies cited above.

Tree and overtopping herb cover affect seedling microsites by providing shade from solar radiation and increasing daily minimum temperatures, thereby enabling greater photosynthesis in emergent seedlings of the conifer species we evaluated (Germino & Smith, 1999; Maher, Germino & Hasselquist, 2005). Clear skies lead to nocturnal frost followed by intense sunlight at high elevations in the Rocky Mountains. Exposure to frost followed by bright sunlight resulted in low-temperature photoinhibition and corresponding depressions in photosynthesis for seedlings growing in exposed sites in ATEs (Germino & Smith, 1999; 2000). Greater enhancement of seedling establishment by tree compared to herb cover (Figure 4, Table I) may reflect a less favourable balance of negative and positive effects of herbs compared to trees on young conifers. Young conifers might generally benefit from shade provided by taller neighbouring herbs, but they are also likely to share root zones and compete for soil resources with herbs. Also, shading from herbs potentially caused suboptimal light where seedlings already had tree cover (Figure 4) or in the relatively tall herb canopies of the Tetons, where seedlings did not have as high an affinity for tree cover compared to the other mountains.

CONIFER SPECIES DIFFERENCES

As predicted from known interspecific differences in photosynthetic tolerances to high light and low temperatures, selective survivorship near trees was greater for *A. lasiocarpa* than either *P. engelmannii* or especially *P. albicaulis* (Figure 5). Previous studies indicated differences in germination requirements among these conifers (Patten, 1963; Young & Young, 1992; Tomback *et al.,* 2001), which could lead to microsite variation in emergence. However, selective survival likely contributed more than selective emergence to differences in %SKY among species, as indicated by dissimilarities in the locations where seedlings of each species emerged and survived (Figure 5). Emergent seedlings of *P. albicaulis* appeared most capable of surviving in and colonizing open meadows of the ATE, whereas survival of *A. lasiocarpa* is more likely to require cover provided by resident trees. Agreement in patterns of seedling survival and photosynthesis described above indicate a potentially significant role for physiological responses to sunlight and temperature in tree establishment patterns in Rocky Mountain ATEs. Specifically, interspecific differences in susceptibility to low-temperature photoinhibition of photosynthesis in emergent seedlings may contribute to microsite differentiation and successional relationships among the conifer species and ATEs we evaluated. Previous literature questioned the importance of limitations to carbon uptake for trees at treeline (Körner, 1998), but small seedlings are faced with much greater carbon requirements for growth than mature trees and therefore likely differ in their physiological responses to ATE conditions.

SUMMARY AND IMPLICATIONS FOR TREELINE

Coexistence of trees in ATEs with other tree and herbaceous species is dynamic and transient, as a result of successional replacement in tree islands and treeline fluctuations over broader spatial and temporal scales (Lloyd & Graumlich, 1997; Callaway, 1998). Our data indicate that limitations to tree seedling survival contribute to stability in the balance of tree and herbaceous cover in ATEs. Seedling mortality does not appear to result from competitive exclusion by neighbouring plants and is instead more likely to result from extreme microclimate conditions in microsites where seedlings are not protected by neighbouring plant cover. Moreover, interspecific differences in seedling requirements for microsite cover correspond with successional relationships among the species.

Feed-forward relationships resulting from positive relationships among trees are likely to alter ATE responses to climate or disturbance (Alftine & Malanson, 2004). Feed-forward effects may be intensified when multiple species with different regeneration niches are involved. For example, resident *P. albicaulis* trees likely have a more positive effect on seedling establishment of *A. lasiocarpa* than their own seedlings. Tree diversity in ATEs of western North America is being affected by widespread loss of adult *P. albicaulis* to the exotic blister rust and successional replacement by *A. lasiocarpa* with fire suppression (Murray, Bunting & Morgan, 2000; Tomback, Arno & Keane, 2001). Although *P. albicaulis* is bird dispersed, significant time might be required for its natural redispersal into mountains where its extermination appears likely, as a result of geographic separation of mountain ranges. Without *P. albicaulis* and the colonizing ability of its seedlings, initiation and formation of new tree islands may be reduced, potentially decreasing rates of afforestation or tree establishment in ATEs following disturbances such as fire. Billings (1969) speculated that sluggish post-fire regeneration of historic high-elevation forests has contributed to the formation of subalpine meadow in the Snowy Range. The Snowy Range was the only ATE with no *P. albicaulis,* and also the ATE with the least extent of advance establishment away from trees (Figures 1 and 3). The importance of individual species that are colonizing specialists is well known for mixed-species forests, such as the role of pin cherry (*Rubus*) in enhancing stability and resilience of northern hardwoods forest over disturbance–succession cycles (Marks, 1973). Successional species such as *P. albicaulis* may also contribute to the long-term, dynamic stability of forest boundaries, such as alpine-treeline ecotones.

Acknowledgements

Funding was provided by a grant from the Andrew Mellon Foundation. R. Moffitt and N. Hasselquist assisted with data collection, and N. Huntly provided helpful comments.

Literature cited

Alftine, K. J. & G. P. Malanson, 2004. Directional positive feedback and pattern at an alpine treeline. Journal of Vegetation Science, 15: 3–12.

Aplet, G. H., R. D. Laven & F. W. Smith, 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology, 69: 312–319.

Bazzaz, F. A., 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics, 21: 167–196.

Billings, W. D., 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. Vegetatio, 19: 192–207.

Billings, W. D. & L. C. Bliss, 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology, 40: 388–397.

Callaway, R. M., 1998. Competition and facilitation on elevational gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos, 82: 561–573.

Canham, C. D., 1988. An index for understory light levels in and around canopy gaps. Ecology, 69: 1634–1638.

Connell, J. H. & R. O. Slatyer, 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist, 111: 1119–1144.

Donnegan, J. A. & A. J. Rebertus, 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. Ecology, 81: 1370–1385.

Germino, M. J. & W. K. Smith, 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. Plant, Cell and Environment, 22: 407–415.

Germino, M. J. & W. K. Smith, 2000. Differences in microsite, plant form, and low-temperature photoinhibition in alpine plants. Arctic, Antarctic, and Alpine Research, 32: 388–396.

Germino, M. J., W. K. Smith & C. A. C. Resor, 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. Plant Ecology, 162: 157–168.

Germino, M. J., N. J. Hasselquist, T. M. McGonigle, W. K. Smith & P. P. Sheridan, 2006. Colonization of conifer seedling roots by fungal mycelium in an alpine-treeline ecotone. Canadian Journal of Forest Research, 36: 901-909.

Grubb, P. J., 1977. The maintenance of species richness in plant communities: The importance of the regeneration niche. Biological Review, 52: 107–145.

Hadley, J. L. & L. K. Smith, 1986. Wind effects on needles of timberline conifers: Seasonal influence on mortality. Ecology, 67: 12-19.

Handa, I. T., C. Körner & S. Hättenschwiler, 2005. A test of the treeline carbon limitation hypothesis by in situ CO_2 enrichment and defoliation. Ecology, 86: 1288–1300.

Hasselquist, N. J., M. J. Germino, T. M. McGonigle & W. K. Smith, 2005. Variability of ectomycorrhizal colonization and its ecophysiological significance for young conifers at alpine-treeline. New Phytologist, 165: 867–873.

Hättenschwiler, S. & W. K. Smith, 1999. Seedling occurrence in alpine treeline conifers: A case study from the central Rocky Mountains, USA. Acta Oecologia, 20: 129–224.

Hitchcock, C. L., A. Cronquist, M. Owenby & J. W. Thomson, 1969. Vascular Plants of the Pacific Northwest, Volume 1: Vascular Cryptogams, Gymnosperms, and Monocotyledons. University of Washington Press, Seattle, Washington.

Johnson, P. L. & W. D. Billings, 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecological Monographs, 32: 105–135.

Knapp, A. K. & W. K. Smith, 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Canadian Journal of Botany, 60: 2753–2761.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia, 115: 445–459.

Lajzerowicz, C. C., M. B. Walters, M. Krasowski & H. B. Massicotte, 2004. Light and temperature differently co-limit subalpine fir and Engelmann spruce seedling growth in partial-cut subalpine forests. Canadian Journal of Forest Research, 34: 249–260.

Lloyd, A. H. & L. J. Graumlich, 1997. Holocene dynamics of treeline forests in the Sierra Nevada. Ecology, 78: 1199–1210.

Maher, E. L., M. J. Germino & N. J. Hasselquist, 2005. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine-treeline ecotone. Canadian Journal of Forest Research, 35: 567–574.

Marks, P. L., 1974. The role of Pin Cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwoods ecosystems. Ecological Monographs, 44: 73–88.

Moir, W., S. G. Rochelle & A. Schoettle, 1999. Microscale patterns of tree establishment near upper treeline, Snow Range, Wyoming, USA. Arctic, Antarctic, and Alpine Research, 31: 379–388.

Murray, M. P., S. C. Bunting & P. Morgan, 2000. Landscape trends (1753–1993) of whitebark pine (*Pinus albicaulis*) forests in the West Big Hole Range of Idaho/Montana, USA. Arctic, Antarctic, and Alpine Research, 32: 412–418.

NRCS SNOTEL Data Network, 2006. National Water and Climate Center. Natural Resources Conservation Service. United States Department of Agriculture, Online [URL] www.wcc.nrcs.usda.gov/snow

Oosting, H. J. & J. F. Reed, 1952. Virgin Spruce–Fir of the Medicine Bow Mountains, Wyoming. Ecological Monographs, 22: 69–91.

Patten, D. T., 1963. Light and temperature influence on Engelmann spruce seed germination and subalpine forest advance. Ecology, 44: 817–818.

Sankaran, M., J. Ratnam & N. P. Hanan, 2004. Tree–grass coexistence in savannas revisited–Insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters, 7: 480–490.

SAS Institute, 1999. SAS version 8, OnlineDoc. SAS Institute, Inc., Cary, North Carolina.

Seastedt, T. R. & G. A. Adams, 2001. Effects of mobile tree islands on alpine tundra soils. Ecology, 82: 8–15.

Smith, W. K., M. J. Germino, T. E. Hancock & D. M. Johnson, 2003. Another perspective for interpreting altitudinal limits of alpine timberlines. Tree Physiology, 23: 1101–1112.

Spence, J. R. & R. J. Shaw, 1981. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. Great Basin Naturalist, 41: 232–242.

Tomback, D. F., 1978. Foraging strategies of Clark's nutcracker. Living Bird, 16: 123–161.

Tomback, D. F., S. F. Arno & R. E. Keane, 2001. The compelling case for management intervention. Pages 3–29 *in* D. F. Tomback, S. F. Arno & R. E. Keane (eds.). Whitebark Pine Communities. Island Press, Washington, DC.

Tomback, D. F., A. J. Anderies, K. S. Carsey, M. L. Powell & S. Mellmann-Brown, 2001. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology, 82: 2587–2600.

Tranquillini, W., 1979. Physiological Ecology of the Alpine Timberline. Springer-Verlag, Berlin.

Van Miegroet, H. V., M. T. Hysell & A. D. Johnson, 2000. Soil microclimate and chemistry of spruce-fir tree islands in Northern Utah. Soil Science Society of America Journal, 64: 1515–1525.

Veblen, T. T., 1986. Treefalls and the coexistence of conifers in subalpine forests of the Central Rockies. Ecology, 67: 644–649.

Young, J. A. & C. G. Young, 1992. Seeds of Woody Plants in North America. Disocorides Press, Portland, Oregon.

Zar, J. H., 1999. Biostatistical Analysis. 4th Edition. Prentice-Hall, Upper Saddle River, New Jersey.