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Authors: Hughes, Nicole M., Johnson, Daniel M., Akhalkatsi, Maia, and Abdaladze, Otar

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Characterizing *Betula litwinowii* Seedling Microsites at the Alpine-Treeline Ecotone, Central Greater Caucasus Mountains, Georgia

Nicole M. Hughes*
Daniel M. Johnson†
Maia Akhalkatsi‡§ and
Otar Abdaladze‡#

*Corresponding author: Department of Biology, Wake Forest University, P.O. Box 7325 Reynolda Station, Winston-Salem, North Carolina 27109-7325, U.S.A.
hughnm5@wfu.edu
†Pacific Northwest Research Station, USDA Forest Service, 3200 SW Jefferson Way, Corvallis, Oregon 97331, U.S.A.
danieljohnson@fs.fed.us
‡Ilia Chavchavadze State University, Faculty of Life Sciences & Tbilisi Botanical Garden and Institute of Botany, 0105, Kojori Rd. 1, Tbilisi, Georgia
§orchisge@yahoo.com
#otarabdaladze@yahoo.com

Abstract

Seedling establishment is an important factor dictating the altitudinal limits of treeline species. Factors which affect seedling mortality and survival, however, have yet to be fully characterized, especially for deciduous treeline species. Here we describe microsite characteristics of successfully established *Betula litwinowii* seedlings at the alpine-treeline ecotone. Possible harmful effects of sky exposure on seedling physiology (i.e. photoinhibition of photosynthesis) were also examined, as well as possible facilitative effects of co-occurring *Rhododendron caucasicum* shrubs on northern slopes and microtopographical depressions (mainly watercourses) in ridgetop meadows. On northern slopes, seedling density was highest in newly exposed soils, with 90% of the youngest seedlings (<2 cm) occurring in patches of rocky, bare, or moss-covered soils within the *Rhododendron* thicket. *R. caucasicum* was not a significant source of shade for *B. litwinowii*, as most seedlings were established 0.25–0.5 m away from the nearest shrub, and shade cover generated by *R. caucasicum* was observed in only 1% of seedlings at midday. On ridgetops, density of *B. litwinowii* was sixfold higher inside microtopographical depressions compared to outside. Sky exposure of seedlings within depressions was similar to northern slopes, ranging from 50% to 87%. Across all microsites, seedlings were most abundant under 70–87% sky exposure. This preference for open microsites, combined with the observation that sustained photoinhibition of photosynthesis ($F_v/F_m < 0.65$) was observed only in the most open microsites (i.e. >80% sky exposure), suggests that sky exposure is likely not a significant factor affecting seedling mortality in *B. litwinowii*, in contrast to results reported for conifer and broadleaf evergreen species at treeline. A higher photosynthetic capacity and a deciduous life history may provide both tolerance and avoidance to the physiological stresses associated with high sky exposure for *B. litwinowii* seedlings, and other factors, such as soil moisture, more likely account for successful establishment within microtopographical depressions and *R. caucasicum* thickets.

Introduction

Seedling establishment is a necessary component of timberline and treeline migration to a new altitude, as well as the contraction or expansion of the subalpine forest (Smith et al., 2003). Yet, mortality during this early life stage (particularly the first year of growth) may be the highest of all life stages (Germino and Smith, 1999; Maher and Germino, 2006; Bader et al., 2007a). For this reason, seedling (and/or ramet) establishment is a particularly important factor influencing the altitudinal limits of treeline species (Smith et al., 2008). Despite the importance of this life stage, however, microsite features associated with successful seedling establishment have yet to be fully characterized, especially for the less common deciduous treeline species. The large majority of research on seedlings at the alpine-treeline ecotone has focused on evergreen, coniferous tree species (e.g. Knapp and Smith, 1982; Anderson and Winterton, 1996; Germino et al., 2002). Because deciduous and evergreen life history strategies involve distinct physiological and structural traits (e.g. differences in water use efficiency, structural and biochemical traits associated with leaf longevity, nitrogen allocation, freezing tolerance, and photosyn-

thetic capacity), it is possible that the factors which most strongly dictate seedling survival (and thus, altitudinal limits) for one group may be very different from those affecting the other.

Betula litwinowii Doluch. is a dominant, deciduous treeline species in the Kazbegi region of the Central Greater Caucasus Mountains (Fig. 1A) (Dolukhanov, 1978; Nakhutsrishvili, 1999). Beyond the timberline (c. 2250 m), individuals of *B. litwinowii* occur in two general habitats: on north-facing slopes dominated by *Rhododendron caucasicum* Pall. shrubs (which extend the treeline up to c. 2500 m; Fig. 1B), and in microtopographical depressions (ranging from small divots to watercourses) on exposed ridgetops (c. 2500 m; Fig. 1C) (Akhalkatsi et al., 2006). The co-occurrence of *R. caucasicum* with *B. litwinowii* has led some to suggest that the *R. caucasicum* provides a nurse-plant benefit to *B. litwinowii* seedlings, as reductions in sky exposure might benefit seedlings by buffering night and daytime temperature extremes, and/or reduce photoinhibition of photosynthesis during early establishment (Dona and Galen, 2007), similar to microsite characteristics associated with conifer seedling establishment at treeline (Germino and Smith, 1999; Maher and Germino, 2006; Akhalkatsi et al., 2006). The effects of micro-
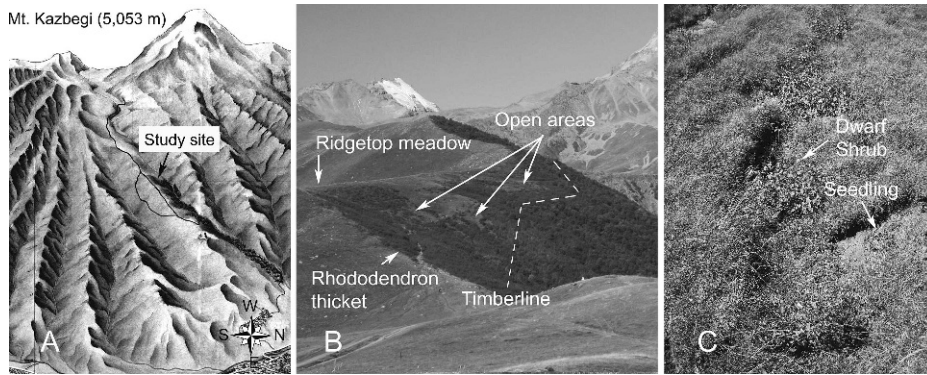
FIGURE 1. Research site. (A) Site map. (B) Northern slope, consisting of (from right to left) timberline, *Rhododendron* thicket with open patches (where *Betula litwinowii* seedlings were most commonly found), and ridgetop meadow. (C) Watercourse on ridgetop with dwarf *B. litwinowii* individuals and seedling.

topographical depressions on seedling establishment are also unclear, though they too may play a role in reducing sky exposure, as seedlings appear to commonly establish only on north-facing depression walls (Akhalkatsi et al., 2006). However, neither of these relationships has been quantitatively assessed, nor have the specific microsites above the timberline in which *B. litwinowii* seedlings are establishing been characterized in any detail. Such information may be valuable for predicting the movement of the alpine-treeline ecotone in a warming climate (e.g. Kullman, 2007), as well as for local re-forestation efforts to remediate human impacts (e.g. over-grazing). Here we characterize the microsites of successfully established *B. litwinowii* seedlings beyond the timberline according to groundcover type, percent sky exposure, photoinhibition of photosynthesis, and proximity to possible facilitative objects (vegetative and topographic). We also evaluate the spatial association between *B. litwinowii* seedlings, *R. caucasicum* shrubs, and topographical depressions to identify possible relationships with successful seedling establishment in *B. litwinowii*.

Materials and Methods

STUDY SITE

The study site is located approximately 400 m above the timberline, at the uppermost elevation in the Kazbegi region of the Central Greater Caucasus Mountains (c. 2498 m a.s.l.; 42°39′N; 44°37′E) at which isolated adult (>1.25 m) birch trees are found. The site is situated at the interface of a continuous ridgetop and north-facing macroslope (42°40′01″N, 44°35′49″E), with *B. litwinowii* forest occurring along the east–west ridgeline extending upwards from the Tergi River valley (c. 1900 m) towards Mt. Kazbegi (5033 m) (Fig. 1A) (Akhalkatsi et al., 2006). The upper altitude limit of the birch forest occurs below the 11°C minimum isotherms of August, although a 9.5°C isotherm occurs in areas protected by snow cover (Nakhutsrishvili, 1999). Vegetation above the timberline is dominated by *R. caucasicum* shrubs on the northern slope, and sedges (*Carex medwedewii* and/or *C. tristis*) on the ridgetop meadow (Fig. 1B). Detailed information on topography, geomorphology, soil, climate, and vegetation of this region is given in Nakhutsrishvili (1999, 2003) and Nakhutsrishvili et al. (2005). The biotope diversity in the alpine-treeline ecotone, as well as a history of the forest vegetation of the Kazbegi region, are also discussed in Nakhutsrishvili et al. (2006). This region of the Central Caucasus Mountains consists of a series of relatively steep, parallel ridges with similar vegetation pattern (birch forests on northern slopes only). All measurements were made in September 2007. Visual inspection of seedlings at the site and general area revealed no evidence of invertebrate herbivory on seedlings; furthermore, grazing livestock were known to have not inhabited

this particular site in recent history, as the area is a designated research site.

SEEDLING MICROSITE CHARACTERIZATION

Seedlings were defined roughly as individuals <25 cm in height (ground to apical tip), and were grouped into four height classes (0–2 cm, 2–5 cm, 5–10 cm, and 10–25 cm). Estimated ages according to node counts were <2 yrs, 2–3 yrs, 3–4 yrs, and 4–7 yrs, respectively. *B. litwinowii* does not reproduce clonally via ramets, therefore all juvenile individuals reported here had developed as individuals from seedlings. All seedlings encountered in individual plots were sampled, which totaled 78 individuals. For each individual, groundcover, percent sky exposure, occurrence in either sun or shade at midday (1100–1500 h), and distance to the nearest potential facilitative object that could have possibly shaded the seedling during germination and early growth were recorded (i.e. topographical structures >3 cm in height, or plant structure >25 cm in height). Groundcover was categorized based on the dominant vegetation and/or soil appearance for the 5 cm radius around the seedling. Groundcover type either consisted of small rocks (<1 cm diameter), bare soil, mossy soil, *Empetrum caucasicum* (a prostrate, mat-forming evergreen dwarf shrub), sedges (*Carex medwedewii* and/or *C. tristis*), or leaf litter. The degree of sky exposure for each individual was quantified based on hemispherical photographs of the canopy taken at seedling heights. Digital images were imported into Gap Light Analyzer software (Version 2.0, Simon Fraser University, Burnaby, British Columbia, Canada, and Institute of Ecosystem Studies, Millbrook, New York, U.S.A.) and used to calculate the fraction of the hemispherical image not obscured by objects (i.e. percent sky exposure). These data were compared to those for two evergreen, conifer species from the Rocky Mountains, U.S.A. (*Abies lasiocarpa* and *Picea englemannii*, adapted from Germino and Smith, 1999), which inhabit environments with similar geologic histories, precipitation, and soil/air temperatures (Bock et al., 1995).

ASSOCIATION BETWEEN B. LITWINOWII AND R. CAUCASICUM

Ten 20 m transects were spaced 10 m apart along the northern slope above timberline where *R. caucasicum* shrubs and *B. litwinowii* co-occur (Fig. 1B). For each transect, ten 1 × 1 m quadrats were spaced at 2 m intervals. Within each quadrat, *B. litwinowii* individuals were counted and assigned an age class based on height: seedling (0–25 cm), juvenile (26–50 cm), small adult (0.5–1.25 m), and adult (>1.25 m). Individuals were recorded as occurring either in the open (>25 cm from the nearest

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Rhododendron), under sparse *Rhododendron* cover (soil covered with *Rhododendron* ramets sparse enough to still see ground beneath), or under dense *Rhododendron* (only *Rhododendron* shrubs visible from eye level; shrubs were pulled back to search for smaller individuals). Seedlings observed in this study were not the same seedlings observed in the microsite characterization study described in the previous section.

TOPOGRAPHICAL EFFECTS ON B. LITWINOWII DISTRIBUTION

In addition to occurring on northern slopes within the *Rhododendron* thicket, *B. litwinowii* seedlings also establish in the exposed, ridgetop meadows above the *Rhododendron* shrubline (Fig. 1B), though establishment appears dependent on the occurrence of 3 cm–1 m microtopographical depressions (formed by freeze-thaw cycles, erosion, and/or watercourses; Fig. 1C). In order to determine whether individuals were more likely to occur in these topographical depressions, ten 20 m transects were spaced 10 m apart along the ridgetop. For each transect, ten 1 × 1 m quadrats were spaced at 2 m intervals. Because of pruning effects on plant morphology (especially height) on the highly wind-exposed ridgetop, height was not always a reliable indicator of relative age, so the terms "seedling, juvenile, young adult, and adult" were not used, though height was still recorded and used to classify individuals. In each quadrat, the number of *B. litwinowii* individuals was recorded according to height class (0–25 cm, 25–50 cm, 0.5–1.25 m), and as either being rooted on flat soil (i.e. not associated with a depression), on a raised area within the depression (flush with flat soil), or within a depression.

SUSTAINED PHOTOINHIBITION OF PHOTOSYNTHESIS

In order to determine whether sky exposure resulted in sustained photoinhibition of photosynthesis, sustained quantum yield efficiency of photosystem II (F_v/F_m) was measured at midday (1100–1300 h) using a PAM Fluorescence System (Hansatech Institute, model FMS-2, Cambridge, U.K.) for all *B. litwinowii* individuals <25 cm in height for which sky exposure measurements had been taken. These values were plotted against percent sky exposure for a total of 46 individuals. Prior to each measurement, one leaf from each individual was dark-adapted for 45 min using model FMS-2 leaf clips, and the seedling's percent sky exposure was measured as described previously.

STATISTICAL ANALYSES

Because this study only characterized seedling microsites on one ridgeline, all replication and corresponding comparisons were within-site. However, visits to additional ridgetop sites in the area revealed an identical vegetation pattern, in general. Regardless, the authors recognize that replication between sites was not carried out in this study.

To determine whether *B. litwinowii* individuals on northern slopes were more likely to be rooted in open soils, under sparse *Rhododendron* canopy cover, or dense *Rhododendron* canopy cover, a Pearson's chi-square test was used to compare total numbers of individuals observed in each site type versus numbers expected under the null hypothesis for each of the three habitat types. Separate tests were run for each of the four age classes. A Pearson's chi-square test was also used to determine whether *B. litwinowii* individuals on the ridgeline were more likely to occur within microtopographical depressions, on raised centers within
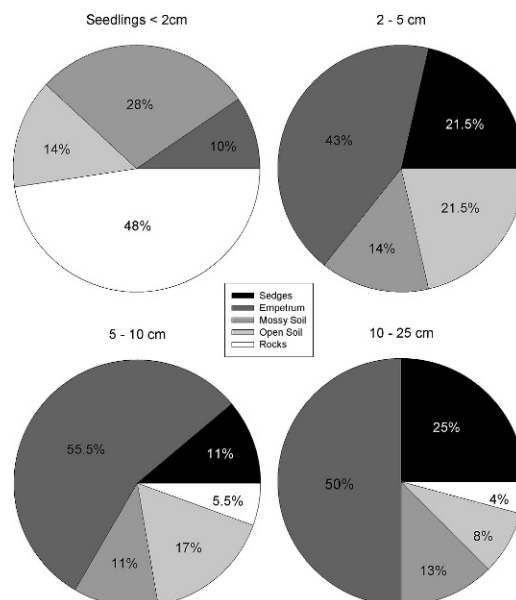

FIGURE 2. Groundcover associated with four age classes of *Betula litwinowii* seedlings. $N = 21$ for seedlings < 2 cm; between 2 and 5 cm, $n = 14$; between 5 and 10 cm, $n = 16$, and seedlings between 10 and 25 cm, $n = 27$.

the depressions, or upon adjacent flat soil microsites. Separate tests were run for each of the three height classes observed. Significance for all tests was determined as $p < 0.05$.

A non-linear regression (modified Hyperbola III) was used to evaluate the relationship between percent sky exposure [independent] to F_v/F_m [dependent] (Sigma Plot V2.0, Jandel Scientific, San Rafael, California, U.S.A.).

Results

GROUNDCOVER AND ASSOCIATION WITH R. CAUCASICUM

The youngest seedlings observed on northern slopes (<2 cm in height) were typically associated with early successional groundcover. Forty-eight percent of seedlings were found among rocks, 14% in open soil, and 28% in moss-covered soil (Fig. 2). *Empetrum caucasicum* comprised the remaining 10% of ground cover associated with these seedlings. Growth of *B. litwinowii* appeared to correspond with procession of groundcover succession, with younger individuals being more common in rocky and moss-covered soils, and older individuals more common among *Empetrum* and sedges (*Carex medwedewii* and/or *C. tristis*) (Fig. 2). Percent values for each of these observations are given in Figure 2.

B. litwinowii seedlings (<25 cm in height) were never observed to be rooted beneath *R. caucasicum* canopies (sparse or dense), but rather, were only rooted in soil with no *R. caucasicum* canopy cover ($\chi^2 = 90$, $p < 0.0001$). Furthermore, seedlings were only rarely observed <5 cm from the nearest *R. caucasicum* shrub (Figs. 3A and 3B), as most seedlings were >25 cm away from the nearest leaf of a *Rhododendron*. The highest density of juvenile (26–50 cm) and young adult (0.5–1.25 m) trees occurred under thin *R. caucasicum* canopies, though this was only significant for young adults ($\chi^2 = 0.82$, $p = 0.67$; and $\chi^2 = 7.2$, $p = 0.028$ for juvenile and young adult trees, respectively). Adults (>1.25 m) were found in similar densities between all site types ($\chi^2 = 2.80$, $p = 0.25$). *B. litwinowii* density for all age classes was lowest in dense *R. caucasicum* canopies.
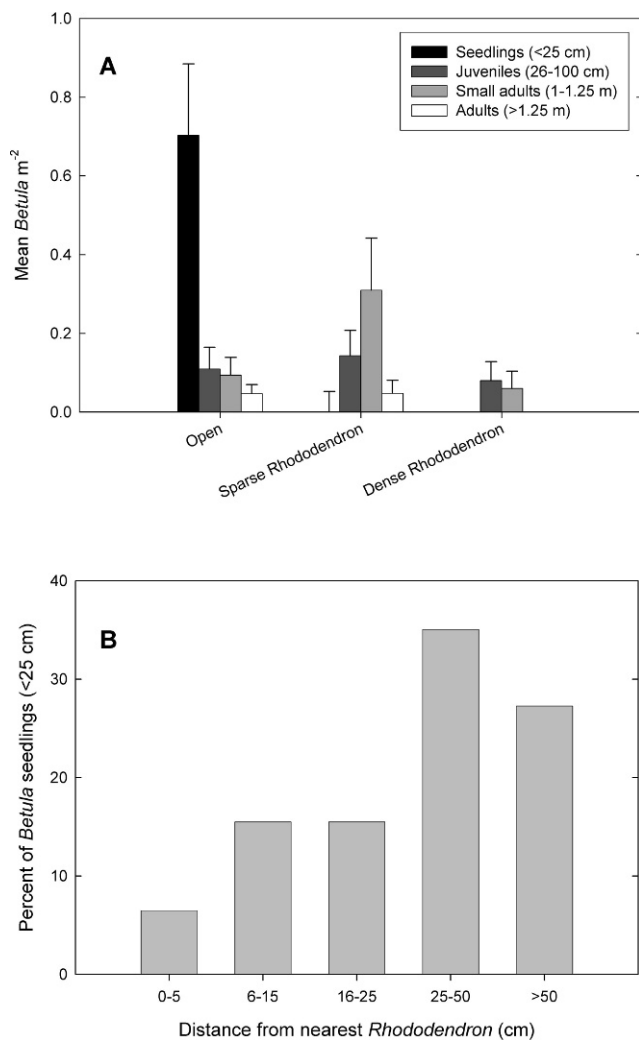
FIGURE 3. Association of *Betula litwinowii* with *Rhododendron caucasicum* shrubs. (A) Mean *Betula* density (by age class) according to *Rhododendron* density in 1 m² transect plots. Open = no *Rhododendron* within 25 cm of individuals. Sparse Rhododendron = individual rooted beneath a *Rhododendron* canopy sparse enough to still see the ground beneath. Dense Rhododendron = individual rooted beneath a *Rhododendron* canopy too dense to see ground beneath without moving branches. (B) Percent seedlings (individuals < 25 cm in height) observed at incremental distances from the nearest leaf of a *Rhododendron* shrub (*n* = 77).

ASSOCIATION WITH MICROTOPOGRAPHICAL DEPRESSIONS ABOVE THE RHODODENDRON SHRUBLINE

Mean *B. litwinowii* density for all three age classes observed was over sixfold higher in microtopographical depressions than either on raised areas within the depressions or on flat soil—a difference which was highly significant for all 3 height classes (χ^2 = 35.7 for individuals 0–25 cm in height, 29.4 for individuals 25–50 cm, and 7 for individuals 0.5–1.25 m, with 2 degrees of freedom; $p < 0.0001$, $p < 0.0001$, and $p = 0.0302$, respectively) (Fig. 4). On average, *B. litwinowii* density in depressions was 0.33 individuals m⁻² for trees <25 cm in height, 0.33 for trees between 25 and 50 cm in height, and 0.06 for trees between 0.05 and 1.25 m in height. On raised areas within depressions, only 0.05, 0.08, and 0.01 individuals m⁻² were observed for these three height classes respectively, and for flat surfaces, 0.04, 0.04, and 0 individuals m⁻². No trees taller than 1.25 m were observed on ridgetops, as
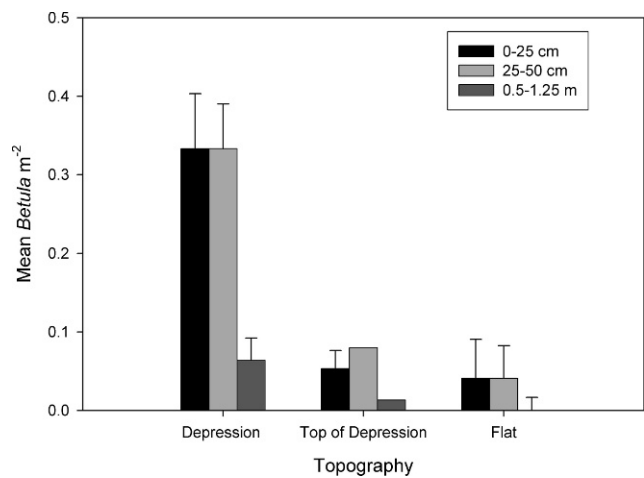

FIGURE 4. Association of *Betula litwinowii* with topographical depressions on ridgetop meadows. Bars represent mean number of individuals (according to height) observed in 1 m² transects rooted either (1) within a topographical depression, (2) on top of the raised soil within a polyhedral depression, or (3) on flat soil (not associated with a depression).

the majority of *B. litwinowii* observed on the ridgetops were dwarf individuals <50 cm in height (likely due to pruning effects of high wind).

SKY EXPOSURE AND PHOTOINHIBITION

B. litwinowii seedlings were observed more frequently in microsites on northern slopes characterized by moderately high sky exposure. Seedlings <25 cm in height were only observed in microsites characterized by 45–86% sky exposure (Fig. 5A). The greatest proportion of the seedlings observed were in sites with 70–79% canopy openness (41%), followed by 80–89% (30%). A comparison of these data with those for two evergreen, conifer species (*Abies lasiocarpa* and *Picea englemannii*, adapted from Germino and Smith, 1999) is shown in Figure 5B. Fluorescence data showed that the majority of *B. litwinowii* seedlings only exhibited mild sustained photoinhibition (as evidenced by F_v/F_m values between 0.69 and 0.80) at midday (Fig. 5C; $r^2 = 0.33$, $p < 0.001$.). However, some seedlings in the most exposed sites (i.e. greater than 80% sky exposure) did show more drastic declines in F_v/F_m (down to 0.50), suggesting a greater degree of photoinhibition of photosynthesis. At midday (1100–1300 h), 54% of seedlings observed were in full sunlight, 37% were in shade provided by topography, and only 8.6% were in shade provided by vegetation (usually other *B. litwinowii*; only once was a seedling observed to be in the shadow of a *R. caucasicum* shrub) (Fig. 5D).

Discussion

Young *B. litwinowii* individuals (<25 cm in height) occurring on northern slopes within the *Rhododendron* shrub thicket were primarily established in open areas with either rocky, open, or moss-covered soils, characterized by 70–90% sky exposure (Figs. 2 and 5A). Seedling age (height) appeared to correspond with groundcover succession in these sites, with young seedlings being found in rocky, bare, and moss-covered soils, and larger individuals among *Empetrum* and sedges (Fig. 2), and eventually, *R. caucasicum* (Fig. 3A). Consistent with this pattern of successional association, *B. litwinowii* seedlings were only rarely observed growing closer than 5 cm in proximity to *R. caucasicum*
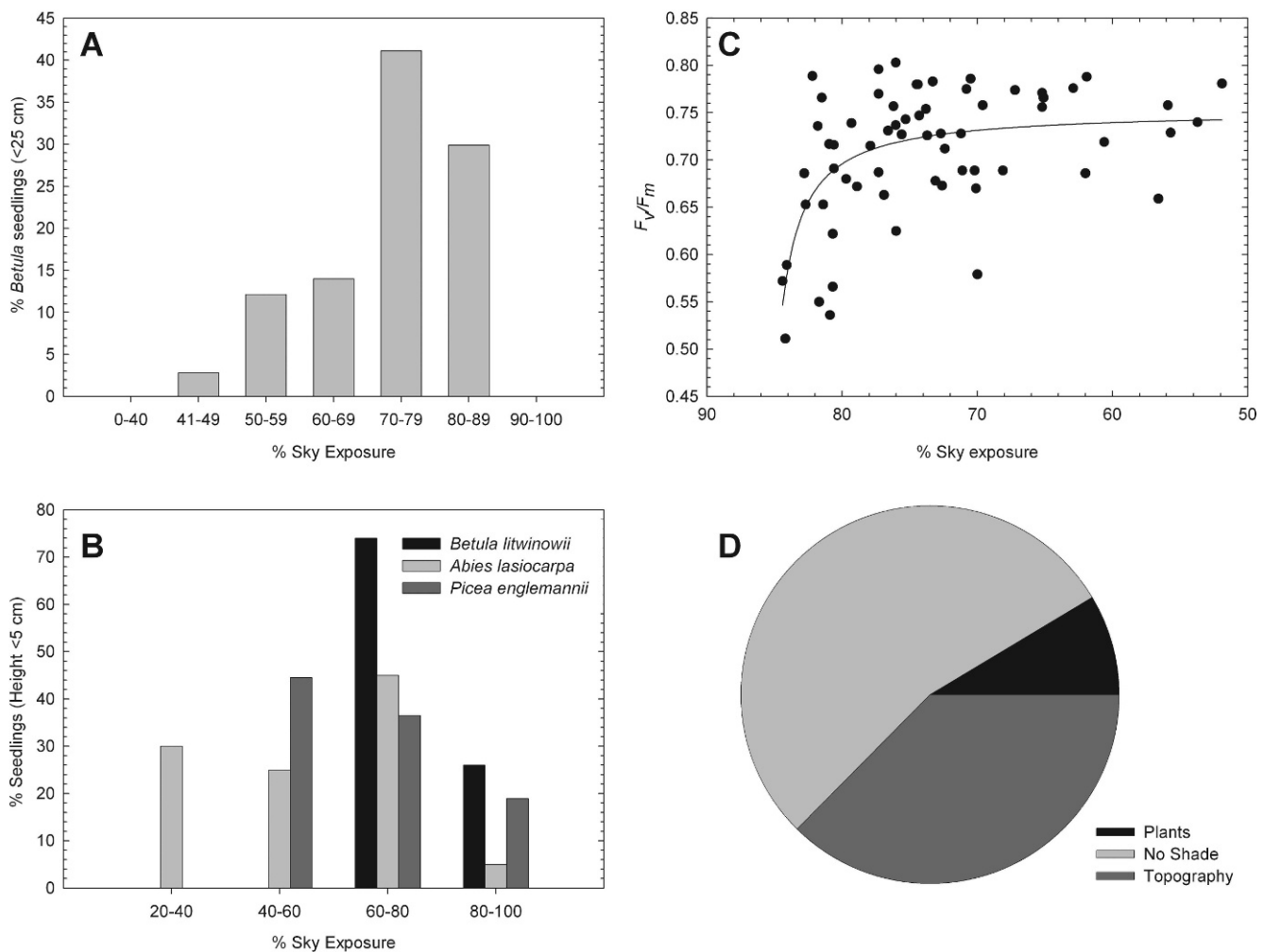
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FIGURE 5. *Betula litwinowii* seedling distribution and sustained photoinhibition according to sky exposure. (A) Seedling distribution according to sky exposure of all *Betula* seedlings observed (height $<$ 25 cm) ($n = 107$). (B) Comparison of seedling distribution according to sky exposure for *Betula*, compared to two evergreen treeline species from the Rocky Mountains, U.S.A. (all seedlings $<$ 5 cm in height). Data for *Abies* and *Picea* adapted from Germino and Smith (1999). (*Betula* $n = 19$; *Abies* $n = 21$; *Picea* $n = 74$). (C) Midday sustained photoinhibition of photosynthesis for *B. litwinowii* as a function of canopy cover (i.e. 1 – sky exposure); $r^2 = 0.33$, $p < 0.001$. (D) Percent of seedlings observed at midday (between 1100 and 1300 h) either exposed to full sunlight ("No Shade"), in shade provided by plants ("Plants"), or in shade provided by topography ("Topography"); $n = 77$.

shrubs (a later successional species), with most seedlings being found from 0.25 m to over 1 m from the nearest leaf of any *R. caucasicum* shrub (Figs. 3A and 3B). Only older individuals of *Betula* ($>$25 cm) were found rooted beneath *R. caucasicum* canopies, suggesting that *Rhododendron* established later than *Betula* in these microsites. Furthermore, densities of all age classes of *B. litwinowii* were lowest among dense *R. caucasicum* shrubs (Fig. 3A). These data, combined with the observation that over 50% of seedlings were in full sunlight at midday, and that shade, when present, was more commonly due to topography (steep slope and northern aspect) than vegetation (Fig. 5D), suggest that *B. litwinowii* seedlings are most likely not dependent on shade from *R. caucasicum* shrubs for establishment as suggested in Akhalkatsi et al. (2006). Rather, it appears that the understory environment of *R. caucasicum* shrubs is inhibitory to seedling germination. These results are consistent with those of Shrestha et al. (2007), who showed that seedlings of *Betula utilis* (another treeline species) could not establish under their own closed canopy.

The absence of the youngest seedlings beneath *Rhododendron* canopies may be attributed to such factors as a lack of open soil due to a dense litter layer (possibly inhibiting radicle establish-

ment), decreased moisture in the leaf litter, potentially allelopathic chemicals (Nilsen et al., 1999), burial under litter (Lei et al., 2002), and/or a lack of sufficient sunlight penetrating the overstory canopy (Catovsky and Bazzaz, 2000; Lei et al., 2002; Thomas et al., 2002). The absence of *B. litwinowii* above timberline on north-facing slopes lacking *R. caucasicum* (Nakhutsrishvili, 2003), however, suggests that either *Rhododendron* and *Betula* have overlapping habitat preference, or that *Rhododendron* enhances *B. litwinowii* survival above timberline by some other means. For example, it is known that *Rhododendron* increases snow capture on northern slopes during winter, and moisture trapping is another common means by which nurse plants may facilitate seedling survival (e.g. Castro et al., 2004). Indeed, survival of most birch species is known to be dependent on relatively high soil moisture (Carlton and Bazzaz, 1998), and survival of *B. utilis* has also been shown to correspond with topographical features associated with high soil moisture (e.g. north-facing aspect, watercourses) (Shrestha et al., 2007). Therefore, the significant association of *B. litwinowii* with microtopographical depressions on ridgetops (Fig. 4) may also be due to moisture differences, rather than shading effects, as depressions effectively accumulate blowing

snow and rainfall, but sky exposure at seedling microsites within depressions were sometimes observed to be as high as 83% (data not shown). However, it is also possible that seedlings establishing within these microtopographical depressions are experiencing less herbivory or trampling by grazers or large herbivores than seedlings in the open (Bock et al., 1995), though no grazing is known to have occurred in this site in recent history. Even so, this explanation would only apply to seedlings in the ridgetop meadow, as the *Rhododendron* thicket is generally impenetrable to livestock.

One of the most striking aspects of the data presented here is the high percent sky exposure characteristic of *Betula* seedling microsites relative to those documented for evergreen, conifer treeline species, such as *Abies lasiocarpa* and *Picea englemannii* (Fig. 5B), and *Pinus albicaulis* (Germino and Smith, 1999; Maher and Germino, 2006). The youngest *B. litwinowii* seedlings (<5 cm) we observed were found only in sites with 60–86% sky exposure— a much more open and narrower range of habitat than has been reported for *Abies*, *Picea*, and *Pinus* spp. seedlings, which generally require shade to establish (Germino and Smith, 1999; Maher and Germino, 2006). Specifically, mean percent sky exposure for *B. litwinowii* seedlings was 74%—a value 10% higher than *Picea* (64%) and 20% higher than *Abies* (54%) (Fig. 5B; data adapted from Germino and Smith, 1999). However, data from Maher and Germino (2006), which include *Abies* and *Picea* seedling data from additional sites, suggest that this difference may be as high as 40% and 50%, respectively. Similarly, seedlings of *Pinus* spp. also appear to establish in more shaded sites, averaging only ca. 27% sky exposure (Maher and Germino, 2006). Artificial shade was also necessary for evergreen tree seedling survival at Ecuadorian treelines in the Andes (Bader et al., 2007a, 2007b) and in the Australian Alps (Ball et al., 1991).

One explanation for *B. litwinowii*'s ability to establish in more sun-exposed sites relative to these evergreen, conifer species is its relatively higher photosynthetic capacity. At the time of study, *B. litwinowii* showed a maximum photosynthetic capacity of ca. 14 μmol CO_2 m^{-2} s^{-1} (data not shown)—40% higher than the average for *Picea* (10 μmol m^{-2} s^{-1}), and 130% higher than *Abies* (6 μmol m^{-2} s^{-1}) (Germino and Smith, 1999). It is known that a decreased capacity for photosynthesis renders plants intrinsically more vulnerable to photoinhibition, due to a reduction in energy sinks available for energy dissipation (i.e. photochemical quenching; Osmond, 1981; Powles, 1984) and may also reduce their capacity for root growth and/or mycorrhizal infection (Cui and Smith, 1991; Miller et al., 1998). Indeed, seedlings and juveniles of species with the highest photosynthetic capacities have been shown to tolerate the greatest sky exposure (Germino and Smith, 2000; Maher and Germino, 2006). Consistent with this explanation, only mild sustained photoinhibition of photosynthesis was observed at midday for the majority of seedlings measured, with midday F_v/F_m values dropping below 0.65 only when percent sky exposure was greater than ca. 80% (Fig. 5C). Because broadleaf and deciduous life histories are both generally associated with higher photosynthetic capacities relative to those of needle-leafed evergreens (Field et al., 1983; Warren and Adams, 2004), such a distinct pattern in treeline seedling microsite preference might be expected.

In addition to a higher photosynthetic capacity, the absence of leaves in deciduous species during colder, more stressful seasons may be another reason *Betula* seedlings are capable of successfully colonizing these more exposed microsites, as perhaps damage incurred during winter stress in evergreens would render establishment in these sites too costly. This idea is supported by high seedling mortality in evergreen treeline species during winter in sites characterized by high sky exposure (Germino et al., 2002;

Maher et al., 2005), as well as the general lack of local evergreen species (*Rhododendron caucasicum*) in the more exposed sites where *B. litwinowii* establishment was observed (such as the ridgetop meadows) (Akhalkatsi et al., 2006). Furthermore, because many of the physiological stresses related to sky exposure are greatest during the winter (e.g. temperature extremes, membrane and molecular destabilization, frost damage, and low-temperature photoinhibition of photosynthesis), deciduous species largely avoid the major consequences of establishing in open microsites. This may therefore be another factor which explains why protection from sky exposure is not as critical for *Betula* seedling survival compared to evergreens (e.g. Ball et al., 1991; Germino et al., 2002; Maher et al., 2005; Maher and Germino, 2006).

In conclusion, although some factors associated with seedlings survival at the alpine-treeline ecotone do appear to be shared between evergreen and deciduous treeline species (e.g. microsites which promote soil moisture), others are in contrast (protection from sky exposure). We have demonstrated that *R. caucasicum* is most likely not facilitating *B. litwinowii* seedling establishment via shading as suggested in Akhalkatsi et al. (2006), although enhancement of snow capture (and thus, protection from extreme winter low temperatures, and enhanced soil moisture from snowmelt) by *Rhododendron* may enhance seedling germination and survival along northern slopes. This explanation is consistent with the occurrence of *B. litwinowii* in microtopographical depressions on exposed ridgetops, though more research is needed on the effects of snow pack accumulation, soil moisture, and temperature to test these hypotheses.

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