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

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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.

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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 photosynthetic 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-

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