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Facilitation of Seedling Microsites by *Rhododendron caucasicum* Extends the *Betula litwinowii* Alpine Treeline, Caucasus Mountains, Republic of Georgia

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Abstract

In the Central Greater Caucasus Mountains, Georgia, *Betula litwinowii* (birch) occurs on north-facing slopes of east-west ridgelines that extend upward to high mountain peaks, forms the alpine timberline at higher elevation, and reaches its highest treeline limit only when associated with the broadleaf evergreen shrub, *Rhododendron caucasicum*. This association might generate an ecological facilitation of either temperatures or sky exposure, both of which have been related to the altitudes at which timberlines/treelines occur. At the lowest site (2072 m) the greatest abundance of birch seedlings (up to 2.3 seedlings/m^2) occurred at shaded microsites beneath the *B. litwinowii* overstory and along shaded north-facing walls of polyhedral soil depressions just beyond this treeline. These seedling microsites also had substantially colder air and soil temperature regimes than more sun-exposed microsites. Similarly, at the highest elevation site (2512 m) the second greatest seedling abundance (0.73 seedlings/m^2) occurred in the shaded understory beneath *R. caucasicum*. Moreover, these microsites had the coldest minimum air and soil temperatures (−1.3°C at 5 cm depths), along with the greatest number of days (40) with minimum soil temperatures <5°C recorded for the measurement period (11 July to 25 October 2003). In addition to the lowest number of seedlings, the more sun-exposed microsites at all sites also had the greatest percent (28–32%) of red leaves per plant, indicative of high concentrations of photoprotective anthocyanins. Thus, reduced sky exposure, and not cold temperature effects, was associated with greater seedling abundance and fewer red leaves per seedling, despite colder temperature regimes. Thus, facilitation of *B. litwinowii* seedling establishment by the *R. caucasicum* overstory appeared to extend the maximum altitude of the *Betula* treeline via reductions in sunlight exposure, despite lower temperatures.

Introduction

The high altitude limits of forest tree growth have attracted the interest of ecologists for over a century (e.g., Pisek and Winkler, 1958, 1959; Billings, 1969; Benecke and Havranek, 1980; Häsler, 1982; Grace, 1989; Wieser, 1997; Gansert et al., 1999; Gansert, 2002). If current projections are accurate, continued global warming may result in the disappearance of a significant portion of the Earth's biodiversity, including the potential replacement of alpine tundra due to encroachment of subalpine forest from below (e.g., Innes, 1991; Rochefort et al., 1994; Kullman and Kjällgren, 2000). Moreover, alterations in species composition and distribution patterns of subalpine forest and alpine plant communities could have major impacts on mountain hydrology and water supply to lower elevations.

While many timberlines world-wide are composed of evergreen conifer tree species, timberlines in the Central Greater Caucasus of Georgia consist of broadleaved, deciduous tree species (Nakhutsrishvili, 1999, 2003). These birch-dominated forests are widespread in the subalpine belt of the Kazbegi region (occurring only on northern slopes at ~2100–2900 m) and are fairly typical of many alpine timberlines found throughout Eurasia. Regionally restricted on the southern limit of its northern hemispheric range by past ice ages, the genus *Betula* comprises a small collection of species in the Caucasus that now dominate the subalpine zone, forming the upper-elevation timberline and treeline (Dolukhanov, 1978; Nakhustrishvili, 1999). *Betula litwinowii* is the dominant timberline species between ~1750 and 2500 m elevation, occurring as monotypic stands at lower timberlines, and mixed with *R. caucasicum* shrubs to form the highest elevation treeline for this birch species.

Air and soil temperatures have been correlated with the altitude at which timberlines and treelines occur world-wide, and more mechanistically with the negative impacts of high altitude on the ecophysiology and growth of timberline trees (see Körner, 2003 for review). Ecological facilitation that reduces seedling sky exposure (cold nighttime sky and excessive daytime sunlight) has also been correlated with successful seedling establishment in the treeline ecotone, an important component of timberline stability (see Smith et al., 2003, for review). The purpose of the present study was to measure and compare air and soil temperatures, as well as incident sunlight that occurred at microsites where seedlings of *Betula litwinowii* Doluch were establishing naturally at typical timberline/treeline sites. Because *B. litwinowii* occurs at its greatest altitude only when in association with *Rhododendron caucasicum* Pall, ecological facilitation of these abiotic factors may be provided by the latter. Seedling abundance, temperature measurements at sun-exposed and shaded microsites (including natural polyhedral soil depressions), and the degree of leaf discoloration (red leaves) were measured for seedlings found at

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