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Authors: Akhalkatsi, Maia, Abdaladze, Otar, Nakhutsrishvili, George, and Smith, William K.

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

*Maia Akhalkatsi**‡*
*Otar Abdaladze**§*
*George Nakhutsrishvili**# and*
William K. Smith†

*Institute of Botany, Georgian Academy of Sciences, Kojori Road 1, 0105 Tbilisi, Republic of Georgia.
†Corresponding author: Wake Forest University, Department of Biology, P.O. Box 7325, Reynolda Station, Winston-Salem, NC 27109-7325, U.S.A.
smithwk@wfu.edu
‡orchisge@yahoo.com
§otarabaladze@yahoo.com
#nakhutsrishvili@yahoo.com

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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all study sites. This red leaf color is now recognized as an indication of high anthocyanin concentrations that provide photoprotection under excessive sunlight incidence, especially when coupled with cold temperatures (see Close and Beadle, 2003 for review; Hughes et al., 2005). These comparisons were also made for microsites generated by *R. caucasicum* in association with *B. litwinowii* at its highest elevation of occurrence. Thus, the possible role of *R. caucasicum* in facilitating the establishment of *B. litwinowii* to its highest elevation limit was evaluated, plus the possible role of temperature and sky sxposure, or both.

Materials and Methods

Six individual study sites were selected that were considered representative of the general types of timberlines/treelines observed for *B. litwinowii* in this region. Measurements of air and soil temperatures at seedling microsites were compared at the highest and lowest altitude study sites, plus the sunniest and most shaded microsites. The abundance of seedlings (no./m^2) and portion of red leaves per plant were also measured at all six study sites. These data were used to evaluate the possible role of *R. caucasicum* in facilitating the establishment and growth of *B. litwinowii* at treeline via alterations in temperature and/or sky exposure. "Treelines" here are considered to be the highest altitude at which an individual of a particular tree species occurs in any growth form; a "timberline" is the highest altitude at which intact subalpine forest occurs, and the "treeline ecotone" is defined as the transitional area between the timberline and treeline (e.g., Smith et al., 2003).

STUDY AREA

The Kazbegi region is located just north of the main watershed for the Central Greater Caucasus Mountains, in the valley of the Tergi River (42°48′N; 44°39′E) near the Russian border. This range is one of the most geomorphologically complex, high-mountain ecosystems of this region (Nakhutsrishvili, 1999), and is composed of alternating ridges and valleys that extend from the valley flow to the higher peaks above (e.g., Kazbegi) in an east-west direction. The elevations of these mountains range between ~1210 and 5033 m (highest peak is Mt. Mkinvartsveri, or Kazbegi) with a mean elevation of 2850 m. Soils of this area consist of Jurassic rocks, Paleozoic and older granites, along with younger lava and moraine deposits.

The flora of the Kazbegi region numbers more than 1100 species of vascular plants, while there are about 6000 species registered in the whole Caucasus and about 4100 of them occur in Georgia (Sakhokia and Khutsishvili, 1975). In particular, this area has one of the greatest diversity of endemic species for any mountain region worldwide (Grossheim, 1936). The *B. litwinowii* (birch) forest is found only on north-facing slopes with continuous winter snow cover and is accompanied by *R. caucasicum*, *Populus tremula*, *Salix kazbekensis*, *Sorbus aucuparia*, *Vaccinium myrtillus*, and *Empetrum caucasicum*, along with other less dominant species. More specific environmental conditions, morphological and functional plant groups, and the composition and productivity of the various plant communities in this region are described in detail in Nakhutsrishvili (2003).

MEASUREMENT SITES

Field investigations were conducted at the top of one of the many ridgelines that begin in the Gergeti River valley (~1900 m) and extend upward toward Mt. Kazbegi (5033 m) (Fig. 2). A total of six measurement sites were chosen as representative timberline/treeline sites of these ridgelines based on observations of the numerous ridgetops of this region (Nakhutsrishvili, 2003). Two treeline sites (Site 1a and 1b) were located at the highest elevation where *B. litwinowii* seedlings and saplings occur (referred to locally as the "true" treeline). At these sites, young seedlings were found in the understory of a *R. caucasicum* shrub thicket, as well as rarely just beyond this shrubline (within ~10 m) on the walls (~10–20 cm heights) of polyhedral soil depressions. Three more sites were established at lower elevation, timberline sites (referred to as "false treelines") that are also typical of this area (Site 2, 3a, and 3b), plus another site (Site 4) inside an intact subalpine forest that is dominated by *B. litwinowii* and forms a characteristic, lower timberline at Sites 3a and 3b. Specific characteristics of each study site are summarized in Table 1 and shown schematically in Figure 2, with additional descriptions below (in order of decreasing elevation):

Site 1a (2512 m: highest elevation treeline ecotone located at the upper elevation limit of birch tree occurrence in the Kazbegi region. Dwarfed and distorted birch seedlings (<0.3 m tall) occur just beyond (<10 m) an *R. caucasicum* shrubline and only on the northern walls of polyhedral soil depressions found throughout a tussock grass meadow. The site is dominated by *Carex medwedewii*, *C. tristis*, *Empetrum caucasicum*, *Festuca supina* (=*F. airoides*), *Kobresia capilliformis*, *Vaccinium myrtillus*, and *V. vitis-idaea*.

Site 1b (2498 m): same location as Site 1a, but below shrubline, and composed of 2- to 3-m-tall birch trees within a densely packed *R. caucasicum* thicket. Associated vegetation include *Alchemilla elisabethae*, *Empetrum caucasicum*, *Sorbus caucasigena* (=*S. aucuparia*), *Vaccinium myrtillus*, and *V. vitis-idaea*.

Site 2 (2248 m): typical of mid-elevation timberline/treeline sites found commonly on steeper north slopes (without *R. caucasicum*) where regeneration of young birch trees and seedlings (~6–10 yr) occurs well below ridgelines. The associated vegetation is a tussock-grass/shrub community dominated by *Anemonastrum fasciculatum*, *Calamagrostis arundinacea*, *Dolichorrhiza caucasica, Salix kazbekensis*, *S. kuznetzowii*, *Stachys macrantha*, *Vaccinium myrtillus*, and *Veratrum lobelianum*.

Site 3a (2164 m): this site and the following site (Site 3b) are within the same treeline ecotone separating intact birch forest and grass meadow, one nearer the timberline (Site 3b) and the other at treeline (this site). This treeline ecotone has a distinct timberline that transitions gradually into a treeline and the adjacent meadow, in contrast to the much more abrupt shrubline at Site 1a. Birch saplings become more dwarfed and distorted further from the timberline and establishing seedlings above treeline were also found only along the walls of polyhedral depressions (identical to Site 1a). Both grasses and herbs dominate this type of meadow, including *Bromopsis variegata*, *Campanula biebersteiniana*, *Carum caucasicum*, *Kobresia capilliformis*, *K. persica*, *Nardus stricta*, and other species.

Site 3b (2155 m): same treeline ecotone as Site 3a, but at slightly lower elevation and closer to the timberline. Here, 2- to 3-m-tall birch trees occur with substantially less dwarfism and distortion in growth form than found at Site 1a, Other forest species mixed with birch are *Salix kazbekensis*, *S. kuznetzowii*, *Sorbus aucuparia*, *Veratrum lobelianum*, etc.

Site 4 (2072 m): located within the understory of the intact birch forest composed of 15- to 18-m-tall trees which form the timberline of Sites 3a and 3b. In addition to birch, the following

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forest species occur as codominants: *Aconitum nasutum*, *A. orientale*, *Populus tremula*, *Swertia iberica* , *Veratrum lobelianum*.

FIELD MEASUREMENTS

The number and locations of all young seedlings (<0.1 m tall) and saplings (1–2 m tall) were recorded within 20 × 20 m plots at all six study sites. At the highest (Sites 1a and 1b) and lowest (Sites 3a and 3b) elevation sites, individual seedlings were categorized as growing in either sun or shade microsites according to the amount of incident PPFD (photosynthetic photon flux density in mol m^{-2} s^{-1}; 0.3 to 0.7 μm wavelengths) measured. At each site, air and soil temperatures were made from 11 July to 25 October 2003 (within ~10 cm of individual seedlings) with the greatest or least values of daily PPFD determined from measurements taken every 10 min (~0800 to 1730 h solar time) on clear days (8, 9, and 11 July). These highest and lowest elevation sites (Sites 1a, 1b, and 3a, 3b) were then compared for differences in incident sunlight, as well as air and soil temperatures, for the three most sun-exposed and shaded microsites (determined from PPFD values) where seedlings were found.

Seedling ages at all sites were estimated from the number of primary branch nodes and the widths of main stems (with ring counts) and primary shoots. The amount of leaf discoloration (reddish) for individual seedlings/saplings was determined by counting the percent of red leaves (>1/4 of the total leaf surface area reddish) per seedling. The compass location of each of the six study sites, plus corresponding slope exposure and inclination, were measured using a global positioning system and compass-clinometer (Etrex Summit, Garmin, Switzerland, and Recta DP 6, Switzerland, respectively).

PPFD was measured using quantum sensors (Model 190S, LICOR Inc., Lincoln, Nebraska, USA) placed at seedling heights (mid-height of leaf crown) next to individual seedlings (within ~20 cm) and with the sensor plane oriented horizontally. PPFD sensors were also within 20 cm of the air and soil temperature sensors. Mean hourly values were computed from data logger measurements taken every 10 min during the day on clear days throughout summer (11 July to 25 October 2003).

Air and soil temperatures adjacent (within 20 cm) to natural field seedlings in the three most exposed and shaded microsites at all sites (Fig. 2) were monitored from July 11 through 25 October 2003. Air temperatures were measured with shielded thermocouples (fine-wire copper-constantan, 26 ASU gauge) at seedling heights, along with soil temperatures from thermocouples buried at 5 cm depths, in both sun-exposed and shade microsites. Mean hourly values were computed from measurements taken every 10 min using data loggers (Onset StowAway Tidbit, USA; Squirrel 1200, Grant Instruments, Cambridge, England). Mean values and standard deviations were calculated for all temperature and PPFD data, while statistical comparisons of mean values among sites and microsites were accomplished using a one-tailed Students *t*-test or ANOVA for multiple comparisons of mean values among sites (Zar, 1999).

Results

MESOCLIMATE

The mesoclimate of the Kazbegi area is considered cool-temperate with an annual mean air temperature near 5°C based on a 26-yr record (Fig. 1; Nakhutsrishvili, 2003). The daily mean air temperature during the coldest month (January) is −11°C with minimums near −30°C. Mean air temperature during the warmest

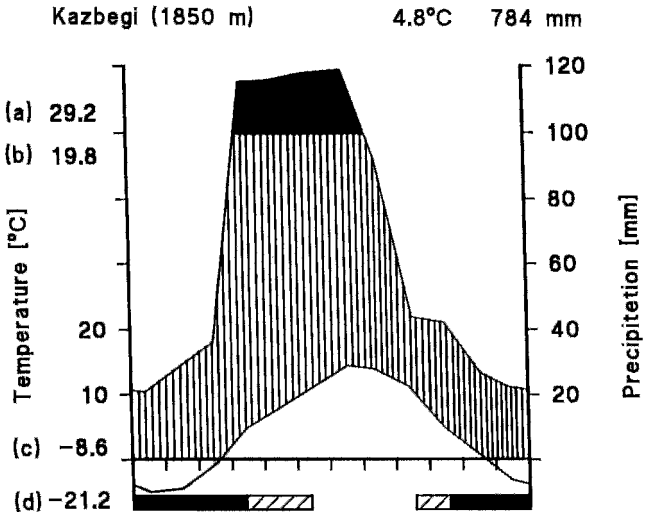


FIGURE 1. Climate diagram (12-yr record) for the town of Kazbegi (42.65°N, 44.63°E; 1850 m elevation), Republic of Georgia, derived from a weather station located within 3 km of the six study sites, but at slightly lower elevation (1850 m). Lower curve is mean monthly air temperature (left axis); upper curve is mean monthly precipitation (right axis) showing the mean period of months with snowfall (hatched) versus rainfall (dark). Horizontal black bars at bottom indicate the mean winter frost period; hatched bars show the mean occurrence of minimum temperatures below freezing. Additional temperature data are as follows: maximum air temperature, 29.2°C; minimum air temperature, −21.2°C; mean daily maximum of warmest month, 19.8°C; mean daily minimum of coldest month, −8.6°C.

months (July and August) is near 15°C (maximums near 30°C). Stable snow cover persists for 5 to 7 mo from November to May, reaching its maximum depth of 1.2 m in March. The average annual precipitation is about 1000 mm with peak values in early summer; ground fog is frequent in the zone (12-yr mean of 135 d yr^{-1}), especially following clear nights in summer.

MICROCLIMATE

PPFD

Integrated PPFD was nearly double (mean of 81 versus 44% of full sunlight, respectively) for sun-exposed compared to shaded understory microsites for all study sites with an overstory of either *R. caucasicum* (Site 1b) or *B. litwinowii* (Sites 3b and 4) when integrated over midday measurement intervals (N = 18 for sun-exposed microsites and 15 for shade microsites). Also at Sites 1a and 3a, corresponding mean midday PPFD measured at young seedling locations within polyhedral depressions (north-facing walls) averaged 562 ± 245 μmol photons m^{-2} s^{-1} at midday (1100–1400 h) versus 2308 ± 98 μmol photons m^{-2} s^{-1} (N = 24) above sky-exposed, adjacent soil surfaces outside depressions (within ~20 cm), on clear days in July and August (N = 19) (Table 2).

Air and Soil Temperatures

At slightly lower elevation than the six study sites (~200 m), the town of Kazbegi experiences approximately seven months of non-freezing minimum temperatures from mid-March to mid-September, although freezing temperatures have occurred until mid-May and began again in mid-August (Fig. 1). Mean maximum air temperatures below 15°C have occurred in mid-

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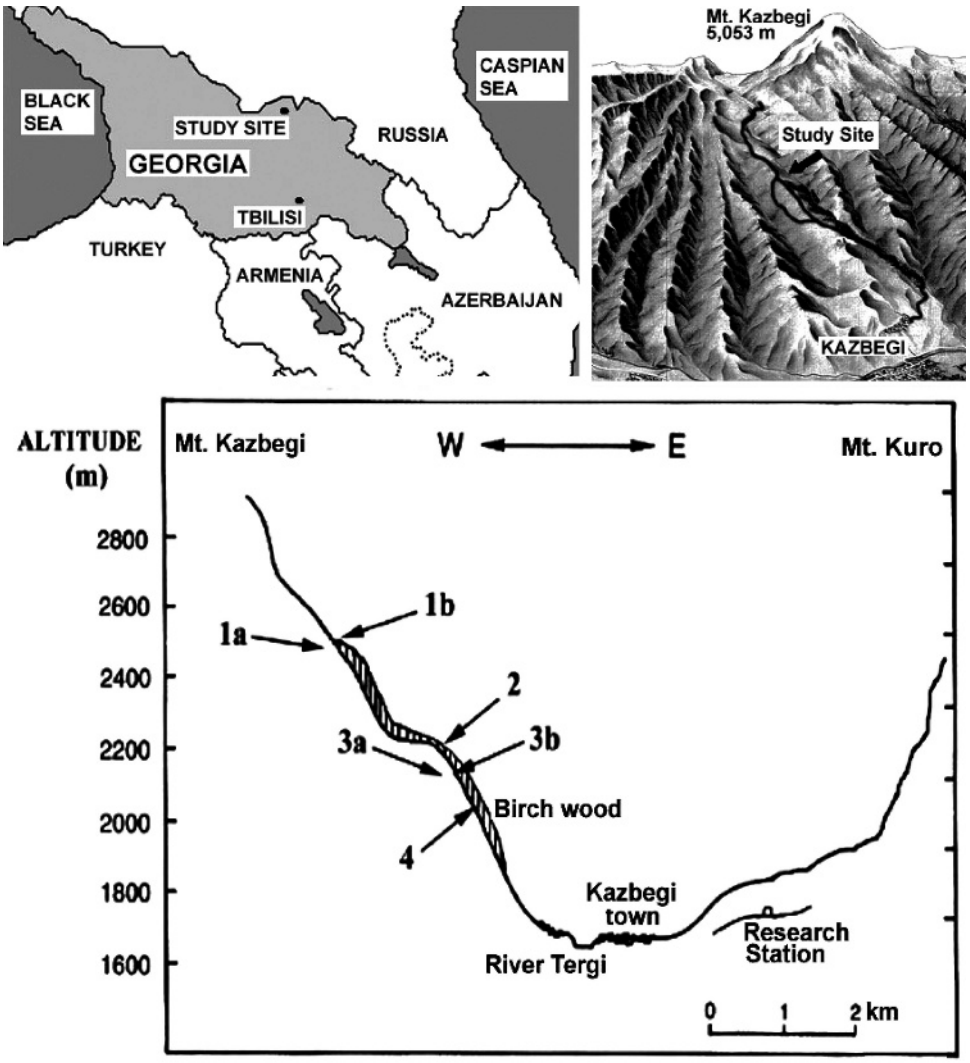


FIGURE 2. Maps showing the geographic location of Georgia and location of study area (upper left), the landscape (repeating parallel ridges) of the study area (upper right), and a schematic profile of the six study sites (bottom), all located within 10 km of the town of Kazbegi (approximately 120 km north of the capital Tbilisi) in the Central Caucasus Mountains very near (~25 km) the Russian border. This landscape consists of ridges and valleys that begin in the Tergi River Valley and extend upward toward Kazbegi Peak. Birch forests (*B. litwinowii*) occur only on the north-facing slopes of these ridgelines and are mixed with *R. caucasicum* at the upper limits of the birch treeline.

June to mid-July, while maximum and mean maximums for the warmest months are considerably higher (29.2°C and 19.8°C, respectively). Minimum annual air temperatures are typically below −20°C.

For the six study sites at higher elevation, mean daytime air and soil temperatures were lowest within the understory of *R. caucasicum* at the highest site (Site 1b). Sun-exposed seedling microsites were generally warmer than shade microsites at all study sites, except for the intact birch forest site (Site 4) (Fig. 3). More specifically, air temperatures at sun microsites were significantly greater (up to 5.1°C at Site 3a), while sun and shade microsites at the highest elevation site (Site 1b) had the lowest mean daytime air and soil temperatures of all sites ($P = 0.01$, ANOVA). Also, air and soil temperatures at the two higher elevation sites (Site 1b and Site 2) were greater than soil temperatures (up to 11.9°C at Site 2). This was *not* the case for the lower elevation sites (Sites 3a, 3b, and 4) where soil temperatures in sunny microsites were nearly the same, or considerably higher than air temperature. The smallest differences between air and soil temperatures occurred in the understory of the intact birch forest of Site 4. Air and soil temperature differences between sun and shade microsites were statistically different ($P = 0.01$, ANOVA) within each site, except for the birch understory site (Site 4) (Fig. 3).

Soil temperatures for sun-exposed microsites of the undisturbed soil surface were substantially warmer compared to the more vertically oriented edges of natural polyhedral depressions where *B. litwinowii* seedlings occurred (Sites 1a and 3a) (Fig. 4; Table 2). In addition, these exposed microsites had substantially greater variation in daily maximum and minimum temperatures.

TABLE 1

Characteristics of study sites in the Kazbegi Region, Central Greater Caucasus Mountains, Republic of Georgia.

Study Sites	1a	1b	2	3a	3b	4
Lat/Long N	42°40′01″	42°40′01″	42°39′55″	42°39′56″	42°39′56″	42°40′02″
S	44°35′49″	44°35′49″	44°36′40″	44°37′04″	44°37′05″	44°37′09″
Altitude (m)	2512	2498	2248	2164	2155	2072
Slope azimuth	12°N	6°N	19°N	22°N	21°N	26°N
% plant cover	95	90–95	90–95	90	85–90	70–75
R. caucasicum	no	yes	no	no	no	no

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TABLE 2

Incident sunlight (PPFD) and the number of days during the measurement period (11 July–25 October 2003) that mean maximum and mean minimum daily soil temperatures (5 cm depth) were above or below the indicated temperatures (°C) at the highest treeline (Sites 1a and 1b) and lowest timberline sites (Sites 3a and 3b). PPFD units are mean kmol photons m^{-2} s^{-1} measured at midday (1100 to 1400 h Solar Time) under clear skies. S indicates a seedling microsite on a sun exposed, undisturbed soil surface; D indicates the walls of polyhedral soil depressions; and U represents an understory site (*R. caucasicum* overstory at Site 1b and *B. litwinowii* overstory at Site 3b). Continuous temperature data for Site 3a are shown in Figure 3.

	PPFD			No. days >20			15—20			<5			T_{max}			T_{min}		
Site	S	D	U	S	D	U	S	D	U	S	D	U	S	D	U	S	D	U
1a	2.3	0.4	—	1	0	—	15	3	—	35	19	—	22.1	17.7	—	2.4	0.9	—
1b	—		0.5	—	—	0	—	—	9	—	—	40	—	—	17.4	—	—	−1.3
3a	2.2	0.5	—	19	0	—	18	0	—	16	3	—	25.8	16.1	—	0.3	3.1	—
3b	—	—	0.5	—	—	1	—	—	19	—	—	2	—	—	25.1	—	—	4.0

Similar patterns of temperature variation occurred at Site 3a, located ~400 m below the highest elevation sites (Sites 1a and 1b) (Fig. 4; Table 2). At the highest elevation site, just beyond the *R. caucasicum* shrubline (Site 1a), the number of days above 20°C was substantially less than at the lowest elevation site (Site 3a) (1 d vs. 19 d, respectively, Table 2). The walls of polyhedral depressions at Site 1a, as well as the understory microsites (Site 3a), did not exceed 20°C on any day. Similarly, maximum soil temperatures were lower at Site 1a (22.1°C) than Site 3a (25.8°C), and temperatures measured in the depression walls where seedlings occurred were considerably lower than the adjacent surface soils at both sites (16.1°C and 17.7°C, respectively) (Table 2). The number of days surface soil temperatures were <5°C (35 d) at the highest elevation site (Site 1a) was over twice the number of days (16 d) at the lowest elevation site (Site 3a), while differences were even more evident between the two sites (19 vs. 3 d, respectively) (Table 2). Minimum soil temperatures for the undisturbed soil surface were also higher at Site 1a (2.4°C) than Site 3a (0.3 °C), although the reverse was true for depression wall temperatures (3.1 vs. 0.9°C, respectively). The greatest number of days <5°C (40 d), along with the coldest minimum soil temperature (−1.3°C), occurred beneath the *R. caucasicum* understory at the highest elevation Site 1b (Table 2).

SEEDLING ABUNDANCE AND LEAF COLOR

Seedlings from 1 to 12 yr old were found at all study sites, ranging from a low mean abundance of 0.14 seedlings/m^2 at Site 4 (birch forest understory) to a high of 1.52 seedlings/m^2 at the mid-elevation, timberline Site 2 (Fig. 5). The understory Sites 1b and 3b had the next greatest abundance (0.74 and 0.54 seedlings/m^2, respectively), followed by the more exposed Sites 1a and 3a (0.24 seedlings/m^2), and then Site 4. There was no statistical correlation between site elevation and seedling abundance (P = 0.01, ANOVA)

The greatest percentage of red leaves per plant (28 and 35%) was observed on both young seedlings found along the walls of polyhedral depressions beyond the *R. caucasicum* shrubline at Site 1a, and at the farthest extent of the timberline ecotone of Site 3a (Fig. 5). The lowest values for the presence of red leaves (<4%) occurred at the understory sites (Sites 3b and 4) and on the steep north-facing slope of Site 2. Comparing all data, the percent of red leaves on individual birch seedlings was not correlated with altitudinal differences between the treeline and timberline sites, only sun exposure (P = 0.01, ANOVA; Table 2). Interestingly, sun-exposed leaves of the *R. caucasicum* plants located at the shrubline at Site 1a, in particular, also had a distinct red coloration alongside the full length of the adaxial midvein for all

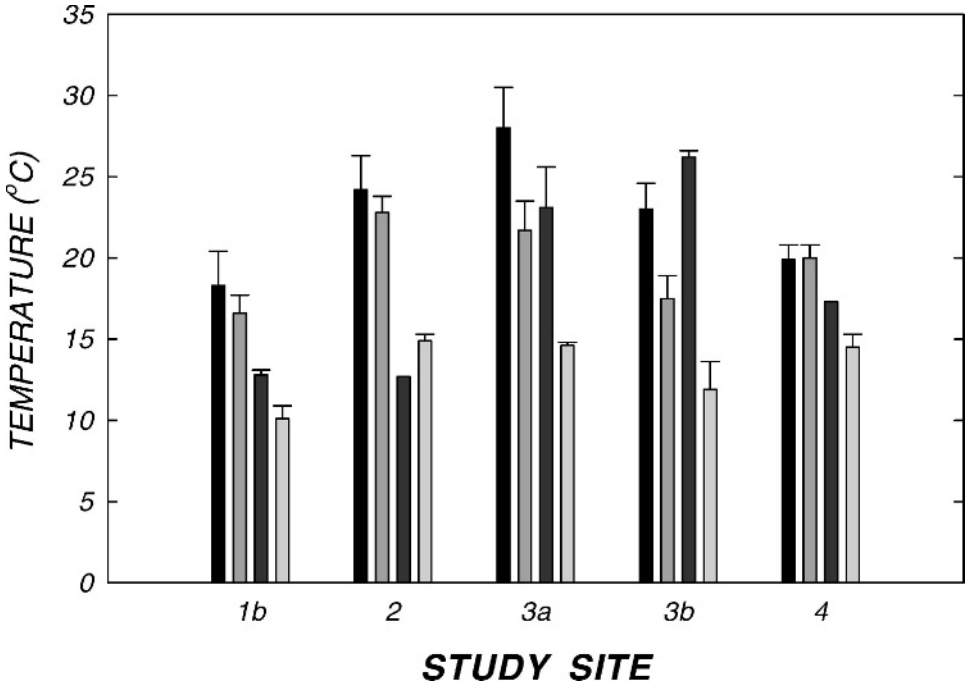


FIGURE 3. Means and standard errors of daytime air (~5 cm above ground level) and soil temperatures (~5 cm below ground surface) measured simultaneously from 1400 to 1600 h on days under mostly clear skies (<20% cloud cover) at the most sunny and shaded microsites measured at each study site. In each group, the order of the bars is (1) T_{air} for sun-exposed microsites, (2) T_{air} for shaded microsites, and (3, 4) are the same conditions for soil temperatures.

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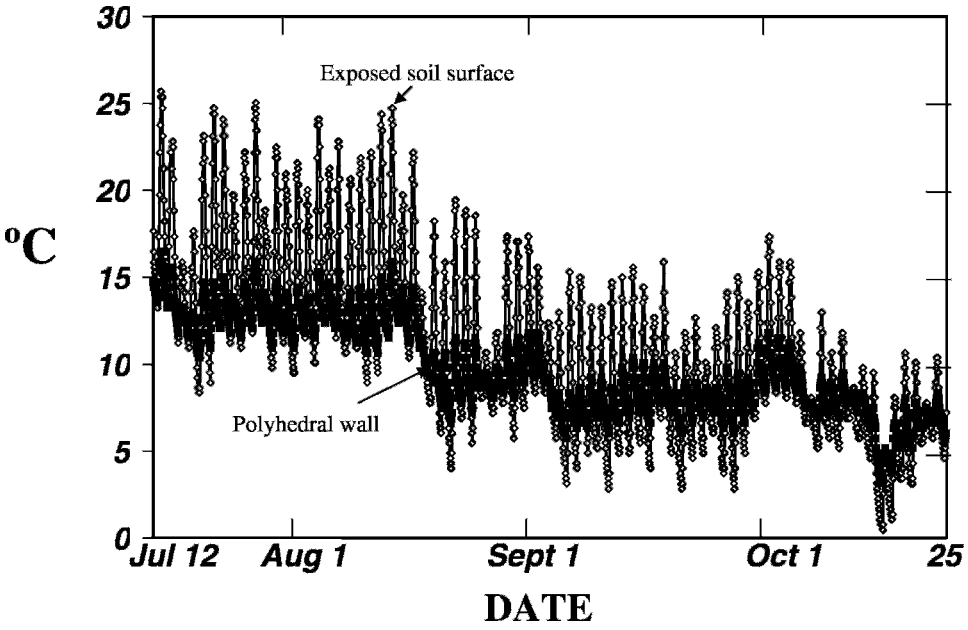


FIGURE 4. Mean hourly soil temperatures (5 cm depth) measured along the sloped (shaded) walls (solid circles) of polyhedral soil depressions where birch seedlings occur, and the adjacent, sun-exposed soil surface (open circles) at Site 3a (2140 m). Each point corresponds to hourly means for measurements taken every 10 min. Virtually identical patterns were measured for the same soil depressions found at Site 1a.

sun-exposed leaves. This area was the only portion of the leaf surface exposed to the direct (perpendicular) rays of the sun due to extreme curling of the leaf margins toward the abaxial surface. The remainder of the leaf surface that was slanted away from direct sunlight remained green. In contrast, *B. litwinowii* leaves at all sun-exposed microsites were more uniformly red across the breadth of the leaf, and tended to occur only on apical and lateral branch tips that were above the *R. caucasicum* canopy.

Discussion

A limitation to the data presented here was the lack of comparisons between measurements for different ridgetop study areas in this area. However, documentation does exist for the distinct vegetation patterns of this area, as well as the existence of the two distinct types of timberlines and treelines in this region of the Central Greater Caucasus Mountains of Georgia (Nakhutsrishvili, 1999). The highest elevation treelines occur almost exclusively on steep ridgetops of north-facing slopes where mature, but stunted, *B. litwinowii* trees occur just below (~10 to 20 m) a *R. caucasicum* shrubline. Birch seedling establishment beyond this shrubline occurs only rarely and is associated with polyhedral soil depressions (~1–2 m on a side) generated by freeze-thaw dynamics of surface soils (frost heave). Both birch seedlings and dwarf saplings can be found along the north- and northeast-facing walls of these depressions (<20 cm deep). These highest treeline sites also have *B. litwinowii* seedlings scattered among the ~0.7- to 1.0-m-tall *R. caucasicum* shrubs that form dense, homogeneous thickets (e.g. Site 1b). In contrast, *B. litwinowii* timberlines at lower elevations occur on northern slopes and usually form a much more gradual and broader treeline ecotone (~20–50 m) composed of dwarfed, crooked-stem trees (~0.3–0.7 m tall) that have increased distortion and diminished size with greater distance from a less clearly demarcated timberline (e.g. Sites 2 and 3a). These individual seedlings/saplings become even more separated spatially as the distance from the forest edge (timberline) to the treeline increases.

Previous studies on *Rhododendron* spp. have focused on its competitive status with other commercially important forest tree species (e.g., Ketskhoveli, 1959; Nilsen et al., 1999, 2001), although recent studies have shown little or no competitive interaction, as well as some evidence for a beneficial effect on tree seedlings (e.g., Lei et al., 2002). One study has associated the microclimate of a *Rhododendron* understory with the successful growth and establishment of tree seedlings, attributed specifically to a lessening of incident sunlight and improved water relations (Lipp and Nilsen, 1997). This ecological "facilitation" in the germination and establishment process is in general agreement with the hypothesis that favorable microsites created by the presence of other plant species become increasingly important as the abiotic environment becomes more harsh (e.g., Callaway, 1995, 1998; Kikvidze and Nakhutsrishvili, 1998). For example, at higher elevations where *Abies lasiocarpa* seedlings and saplings were more spatially aggregated with mature *Pinus albicaulis* than at lower elevation, growth rates were higher for aggregated trees versus trees growing in more open sites (Callaway, 1998). Also, the abundance of new seedlings and the subsequent high survival of young seedlings of *Abies lasiocarpa* were highly associated with the reduction of sky exposure by surrounding vegetation in the treeline ecotone of the central Rocky Mountains (U.S.A.). In contrast, newly emerged seedlings of the codominant *Picea engelmannii* germinated in microsites with little protection from sky exposure and had much higher mortality (Germino and Smith, 2000a, 2000b).

Recent hypotheses of timberline causation have included the possibility that low soil temperatures may result from the large, forest-tree stature and the inherent shading of the soil surface (Körner, 1998). In contrast, the relatively high abundance of birch seedlings beneath the *R. caucasicum* canopy (Site 1b), despite having the lowest minimum temperatures and the greatest number of cold days among all sites, seems to contradict any negative effects of cold soil temperatures. However, the polyhedral depressions of Site 1a and 3a, where birch seedlings were found rarely, also had more constant soil temperatures (higher minimums and lower maximums) than the adjacent soil surfaces, implicating more constant soil temperatures as a possible influencing factor in successful seedling establishment (Fig. 3, Table 2). Furthermore, either microtopography (polyhedral soil depressions), or the shade generated by the overstory canopy, were responsible for reducing incident sunlight levels. This combination of low temperature and high sunlight incidence have been

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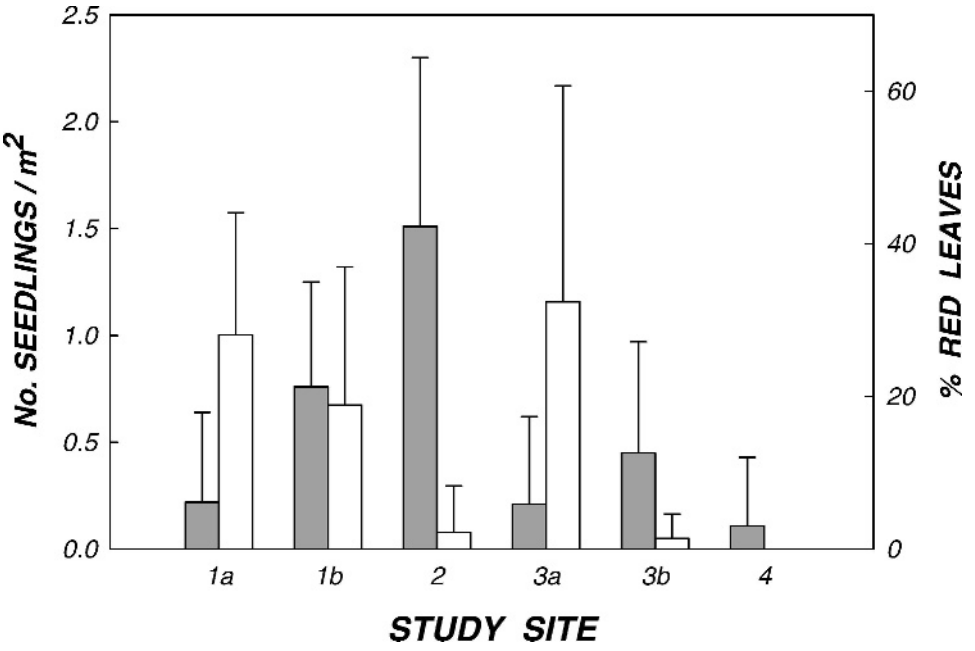


FIGURE 5. Mean number of *R. litwinowii* seedlings per m^2 (solid bars) and the mean percentage of red leaves per plant (open bars) at the six study sites. Mean values for abundance at Sites 1b and 2 were significantly different from the other sites ($P < 0.01$; $N = 10$; ANOVA). Mean values for red leaves at Sites 1a, 1b, and 3a were also significantly different from the others ($P < 0.05$; $N = 40$; ANOVA). Vertical bars are standard errors and zero values are data, not missing measurements.

associated previously with severe limitations to photosynthesis in tree seedlings at alpine treeline which led to low survival, both of which were hypothesized as critical components of timberline/treeline stability (Germino and Smith 2000, Smith et al., 2003).

Finally, seedlings, saplings, and young trees growing in more sun-exposed microsites had a substantially higher number of reddish leaves per plant. This form of leaf color change has been associated with exposure to high sunlight regimes and physiological photoprotection of chlorophyll, especially when in association with low nighttime air temperatures that may approach freezing even in summer (Close and Beadle, 2003; Hughes et al., 2005). However, Site 1b had a relatively high number of seedlings/saplings, as well as a high percentage of red leaves per plant. In explanation, these birch seedlings were generally over 1 m in height and all leaves were positioned above the *R. caucasicum* leaf canopy in full sunlight. The high seedling abundance at Site 2 (steep north-facing slope descending from the ridetop) and low occurrence of red leaves was also associated with low incident sunlight, as well as a typically prolonged snow cover that persists into early summer.

In summary, the observation that these birch trees occur only on northern, lee slopes, where a deeper winter snowpack accumulates, may reflect the ecophysiological intolerance of this species to high sunlight exposure in such a cold environment, as measured for timberline conifer seedlings elsewhere (see Smith et al. 2003 for review). Moreover, *R. caucasicum* shrubs appear to facilitate birch seedling establishment at a higher elevation, similar to the microtopographic effects of polyhedral depressions, extending the highest elevation of occurrence (treeline) for this species and area. This facilitation includes greater shade during the day, along with an avoidance of cold night skies and warmer minimum temperatures for establishing birch seedlings, as evidenced by the warmer nighttime temperatures measured for the walls of the polyhedral soil depressions (Fig. 4). However, the treeline understory site (Site 1b) also produced the greatest number of cold days and the lowest mean minimum air and soil temperatures for the measurement period (11 July to 25 October 2003). This canopy influence on minimum air and soil temperatures is well-documented, and often attributed to the trapping and accumulation of cold-air inside dense vegetative stands, as well as a lack of convective mixing at night (Ball et al., 1997; Körner, 2003). Nighttime leaf temperatures considerably below air temperatures are possible during exposure to the cold night sky during low convective periods due to the increased dominance of longwave radiation exchange (e.g., Jordan and Smith, 1995). Any disadvantage of colder air or soil temperatures to birch seedling establishment, hypothesized previously as an important factor regulating the maximum elevation of timberline and treelines (Körner, 1998), appeared to be outweighed by the benefits of reduced sky exposure. Germino and Smith (2000b) also reported a similar impact on photosynthesis when shading from cold nighttime skies and daytime sunlight was combined, resulting in substantially lower photosynthesis than either alone.

Other environmental factors may also be involved in the association between *R. caucasicum* and birch seedlings at the highest treeline. For example, aerodynamic effects on snow accumulation by the shrub thicket may also be a crucial advantage to birch seedlings during severe winters (burial) and dry summers (soil moisture), potentially important factors in the formation of conifer timberlines and treelines (see Smith et al., 2003 for review).

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References Cited

Ball, M. C., Egerton, J. G., Leuning, R., Cunningham, R. B., and Dunne, P., 1997: Microclimate above grass adversely affects spring growth of seedling snow gum. *Plant, Cell & Environment*, 20: 155–166.

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Benecke, U., and Havranek, W. M., 1980: Gas-exchange of trees at altitudes up to timberline, Craigieburn Range, New Zealand. *New Zealand Forest Service Technical Papers*, 70: 195–212.
Billings, W. D., 1969: Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio*, 22: 192–207.
Callaway, R. M., 1995: Positive interactions among plants. *Botanical Review*, 61: 306–349.
Callaway, R. M., 1998: Competition and facilitation along elevational gradients of the northern Rocky Mountains, USA. *Oikos*, 82: 561–573.
Close, D. C., and Beadle, C. L., 2003: The ecophysiology of foliar anthocyanin. *Botanical Review*, 69: 149–161.
Dolukhanov, A. G., 1978: Timberline and subalpine belt in Caucasus Mountains, USSR. *Arctic Alpine Research*, 10: 409–422.
Gansert, D., Bakes, K., and Kakubari, Y., 1999: Altitudinal and seasonal variation of frost resistance of *Fagus crenata* and *Betula ermanii* along the Pacific slope of Mt. Fuji, Japan. *Journal of Ecology*, 87: 382–390.
Gansert, D., 2002: *Betula ermanii*, a dominant subalpine and subarctic treeline tree species in Japan: Ecological traits of deciduous tree life in winter. *Arctic, Antarctic, and Alpine Research*, 34: 57–64.
Germino, M. J., and Smith, W. K., 2000a: High resistance to low-temperature photoinhibition in two alpine snowbank species. *Physiologia Plantarum*, 110: 89–95.
Germino, M. J., and Smith, W. K., 2000b: Differences in microsite, plant form, and low-temperature photosynthesis in alpine plants. *Arctic, Antarctic, and Alpine Research*, 32: 388–396.
Grace, J., 1989: Tree lines. *Philosophical Transactions of the Royal Society of London B*, 324: 233–245.
Grossheim, A. A., 1936: Analyz flory Kavkaza [Analyses of the flora of the Caucasus]. *Trudy Botanical Institute of Azerbaijan*, Baku.
Häsler, R., 1982: Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia*, 54: 14–22.
Hughes, N. M., Neufeld, H. S., and Burkey, K. O., 2005: Functional role of anthocyanins in high light winter leaves of the evergreen herb, *Galax urceolata*. *New Phytologist*, 168: 575–587.
Innes, J. L., 1991: High altitude and high latitude tree growth in relation to past, present and future climate change. *The Holocene*, 1: 168–173.
Jordan, D. N., and Smith, W. K., 1995: Microclimate factors influencing the frequency and duration of growth season frost in subalpine plants. *Agricultural and Forest Meteorology*, 77: 17–30.
Ketskhoveli, N., 1959: *Vegetation of Georgia*. Tbilisi: Metsniereba.
Kikvidze, Z., and Nakhutsrishvili, G., 1998: Facilitation in the subnival vegetation patches. *Journal of Vegetation Science*, 9: 261–264.
Körner, C., 1998: A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115: 445–459.
Körner, C., 2003: Carbon limitation in trees. *Journal of Ecology*, 91: 4–17.
Kullman, L., and Kjällgren, L., 2000: A coherent postglacial tree-limit chronology (*Pinus sylvestris* L.) for the Swedish Scandes: aspects of paleoclimate and "recent warming" based on megafossil evidence. *Arctic, Antarctic, and Alpine Research*, 32: 419–428.
Lei, T. T., Semones, S. W., Walker, J. F., Clinton, B. D., and Nilsen, E. T., 2002: Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology, and survivorship. *International Journal of Plant Science*, 163: 991–1000.
Lipp, C. C., and Nilsen, E. T., 1997: The impact of subcanopy light environment on the hydraulic vulnerability of Rhododendron maximum to freeze-thaw cycles and drought. *Plant, Cell, and Environment*, 20: 1264–1272.
Nakhutsrishvili, G., 1999: The vegetation of Georgia (Caucasus). *Braun-Blanquetia*, 15: 1–74.
Nakhutsrishvili, G., 2003: High-mountain vegetation of the Caucasus Region. *In* Nagy, L., Grabherr, G., Körner, C., and Thompson, D. B. A. (eds.), *Alpine Biodiversity in Europe*. New York: Springer, 93–103.
Nilsen, E. T., Walker, J. F., Miller, O. K., Semones, S. W., Lei, T. T., and Clinton, B. D., 1999: Inhibition of seedling survival under *Rhododendron maximum* (Ericaceae): Could allelopathy be a cause? *American Journal of Botany*, 86: 1597–1605.
Nilsen, E. T., Clinton, B. D., Lei, T. T., Miller, O. K., Semones, S. W., and Walker, J. F., 2001: Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and below ground for canopy tree seedlings? *American Midland Naturalist*, 145: 325–343.
Pisek, A., and Winkler, E., 1958: Assimilationsvermogen und respiration der fichte (*Picea excelsa* Link) in verschiedener hohenlage und der zirbe (*Pinus cembra* L.) an der alpinen waldgrenze. *Planta*, 51: 518–543.
Pisek, A., and Winkler, E., 1959: Licht- und Temperaturabhangigkeit der CO_2-Assimilation von Fichte (*Picea excelsa* Link), Zirbe (*Pinus cembra* L.) und Sonnenblume (*Helianthus annuus* L.). *Planta*, 53: 532–550.
Rochefort, R. M., Little, R. L., Woodward, A., and Peterson, D. L., 1994: Changes in subalpine tree distribution in Western North America: Effects of climate and other environmental factors. *The Holocene*, 4: 89–100.
Sakhokia, M., and Khutsishvili, E., 1975: *Conspectus Florae Plantarum Vascularium*. Tbilisi: Chewii.
Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.
Wieser, G., 1997: Carbon dioxide gas exchange of cembran pine (*Pinus cembra*) at the alpine timberline during winter. *Tree Physiology*, 17: 473–477.
Zar, J. H., 1999: *Biostatistical Analysis.* 4th ed. Princeton, N.J.: Prentice Hall, 761 pp.

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