The Altitude of Alpine Treeline: A Bellwether of Climate Change Effects

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Abstract Because of the characteristically low temperatures and ambient CO_2 concentrations associated with greater altitudes, mountain forests may be particularly sensitive to global warming and increased atmospheric CO_2. Moreover, the upper treeline is probably the most stressful location within these forests, possibly providing an early bellwether of forest response. Most treeline studies of the past century, as well as recently, have correlated temperatures with the altitudinal limits observed for treelines. In contrast, investigations on pre-establishment seedlings, the most vulnerable life stage of most tree species, are rare. There appears to be specific microclimatic factors dictated by wind and sky exposure that limit seedling survival, and also generate the distorted tree forms commonly observed at treeline. Seedling survival appears critical for creating the biological facilitation of microclimate at the community level which is necessary for the growth of seedlings to normal tree stature, forming new subalpine forest at a higher altitude.

Abstract Es posible que—a causa de características que están asociadas con altitudes más altas: las bajas temperaturas y las concentraciones ambientales de dióxido de carbono—los bosques en las montañas están extra sensibles al calentamiento global y el aumento de dióxido de carbono en la atmósfera. El borde superior del bosque es probablemente el lugar con la más estrés y proviene uno de los primeros avisos de cómo reaccionará el bosque entero. En el pasado y hoy en día, la mayoría de los estudios del borde del bosque ha conectado la temperatura con los límites de la altitud. En contraste, investigaciones de árboles infantiles son raras, y la infancia de los árboles es el período de vida más vulnerable. Aparece que hay factores micro-climáticos dictados por la exposición del viento y cielo que limitan la sobrevivencia de los árboles infantiles, y que generan árboles deformados observados al borde del bosque. Es más, la sobrevivencia de árboles infantiles es crítica para crear la facilitación biológica del micro-clima en una comunidad arbolada. Esta facilitación es necesaria para el crecimiento de árboles infantiles a árboles maduros, los que forman un nuevo bosque subalpino en una altitud más alta.

Keywords Treeline · Timberline · Ecotone · Seedling · Facilitation · Climate

Introduction

Future impacts of global climate change such as warming temperatures could bring significant alterations in the altitudinal patterns of high-altitude forests and their contiguous alpine zones, potentially altering important ecosystem processes such as the amount and distribution of annual snow accumulation, and water conveyance to agricultural areas and municipalities. Avalanche prevention and protection, decreased reflectance of solar radiation back into a warming atmosphere, plus curtailment of soil erosion and landslides into streams, are only some of the critical benefits provided by mountain forests (McNulty & Aber, 2001; IPCC, 2007). Because the coldest air temperatures and lowest CO_2 partial pressures occur at the highest altitudes at all latitudes, these forests may also be particularly responsive to the most documented global change parameter—elevated atmospheric CO_2. However, some investigators have proposed that associated environmental changes such as increased temperature-related droughts (Stockton, 1984; Graumlich & Brubaker, 1986; Graumlich, 1991; Büntgen et al., 2006) and soil nutrients (e.g. nitrogen, Millard et al., 2007) could overshadow the more direct effects of elevated CO_2.

A large portion of the past and current literature dealing with the global distribution of high-altitude forests has dealt specifically with the question of what environmental factors limit tree occurrence (timberline or treeline) at particular altitudes around the world (e.g. Troll, 1973; Arno, 1984; Wardle, 1974; Tranquillini, 1979; Körner, 2003a; Körner & Paulsen, 2004; Holtmeier & Broll, 2007; review of Weiser & Tuasz, 2007). Causal explanations for observed treeline altitudes have been focused predominantly on field studies of life stages well beyond the seedling establishment phase, despite evidence that the greatest mortality, by far, for most tree species (including treeline species) occur before seedling establishment (e.g. Harcombe, 1987; Zens & Peart, 2003). In general, only episodic diseases and parasite outbreaks affecting much older life stages can match this high mortality rate. It has also been proposed that seedling establishment is a prerequisite to additional seedling establishment that generates, ultimately, the microclimatic facilitation needed for the formation of new forest at a higher altitude (Smith et al., 2003). This lack of study on pre-establishment life stages of trees in the treeline ecotone is understandable considering the difficulty in finding and taking ecophysiological measurements on such small seedlings in the field (i.e. cotyledonous seedlings). Interestingly, past studies on seed biology and seedlings (usually greenhouse-grown) of forest trees dominated early forestry research, focusing primarily on reclamation and regeneration strategies following commercial harvesting (e.g. planting of containerized, glasshouse-grown seedlings). Subsequently, studies of climate change effects such as elevated atmospheric CO_2 also centered on greenhouse and growth-chamber seedlings. A more recent trend has been the study of tree stands and communities under more natural field conditions, e.g. using free-air CO_2 enrichment (FACE) to insure more natural conditions of mass exchange (e.g. Ainsworth & Long, 2005).

In general terms, results from ecophysiological studies inside boundary ecotones separating different communities must bridge to population ecology before future changes in species fitness and, thus, range distribution patterns can be predicted

(Bridle & Vines, 2006; Geber, 2008). Most simply, a high-altitude forest could be considered stable at its upper timberline limit if regeneration is occurring in the understory at the high-altitude edge of the intact subalpine forest, but without any generative activity in the contiguous treeline ecotone. Likewise, poor regeneration potential (no seeds or poor seedbed) inside the upper treeline edge would implicate a shift in the upper treeline toward a lower altitude following the death of the mature tree stand. For some communities, low understory sunlight levels and the requirement for fire-induced germination may also limit advanced tree regeneration. Identical measurements at the lower treeline would enable prediction about whether the forest was undergoing spatial expansion or contraction in its altitude zone. The potentially episodic nature of seed production, dispersal, longevity, and germination, along with seedling survival to establishment, is a complicating feature of understanding treeline stability. For example, League and Veblen (2006) reported that recruitment of ponderosa pine seedlings in a Rocky Mountain (USA) forest-grassland ecotone occurred only 4 years out of the past 40. These recruitment years corresponded to above average radial growth of the local seed-bearing trees, along with increased spring and fall precipitation that coincided with El Niño/Southern Oscillation (ENSO) activity. Regardless, measurements of the ecophysiology and survival of pre-establishment life stages (including germination) in treeline species is a key to understanding the altitude of timberline/treeline occurrence (see below).

What Does Treeline Paleoecology Reveal About the Causes of Altitudinal Limits?

The expanding paleological record of plant distribution patterns provides a much longer time perspective that can also be evaluated based on correlations with reconstructed macroclimatic patterns. However, paleobotanical studies, in general, lack fine-scale temporal and spatial resolution, cannot provide detailed mechanistic information, and do not mirror exactly the temporal and quantitative characteristics of today's global climate change (Giorgi, 2001; Malanson, 2001; Holtmeier & Broll, 2005; IPCC, 2007; Kullman, 2007; Williams & Jackson, 2007). As well, these reconstructions are based on macroclimatic variables such as temperature and precipitation over a broad geographic and temporal scale. Albeit, there is some agreement that altitudinal treelines are currently advancing to higher altitudes, similar to the recognized advance of latitudinal treelines further north in the northern hemisphere (Arno, 1984; Shugart et al., 2001; Juntunen & Neuvonen, 2006; Parmesan, 2006; Holtmeier & Broll, 2007; Weiser & Tuasz, 2007). There are also many anomalies to this trend that appear dependent upon local and regional conditions such as edaphics, the proximity to maritime and orographic influences, herbivory, fire, disease, and anthropogenic influences (see Cairns & Moen, 2004; Weiser & Tuasz, 2007, for review).

Following the treeline retreat of the mid-Holocene, a subsequent altitudinal increase coincided with the end of the Little Ice Age approximately 250 years ago and seems to be continuing today (e.g. Holtmeier, 2003). Unfortunately, most of these data come from the Northern Hemisphere only, although Bader et al. (2007) and Di Pasquale et al. (2008) report on recent findings for Andean treelines. Also,

the exceptions to the recent trend of increasing treeline altitudes has been related to such features as grazing, soil erosion, and the associated lag in regeneration time of a formerly occupied treeline ecotone (Juntunen et al., 2002; Holtmeier & Broll, 2005; Wang et al., 2006). The formation of particularly steep mountain slopes, with inadequate soil development, often show some of the sharpest transitions to the contrasting physiognomy and species composition of the alpine community. Kullman (2007) has suggested that exceptionally warm summers and mild winters over the past decade have resulted in improved establishment of Scots pine (*Pinus sylvestris*) seedlings in the southern Swedish Scandes. However, the specific limitations of either soil water or nutrients to the past, present, and future distribution and species composition of high-altitude forests has not been verified by field studies.

There also appears to be a strong episodic component driving the paleo-record of treeline altitudes, and both abiotic and biotic (ecological competition and facilitation) interactions appear to have been important (e.g. Wang et al., 2006). Current forecasts for future climate change predict that episodic events will increase in both intensity and frequency within the framework of a warmer, more energetic atmosphere (Goldenberg et al., 2001; Hayden & Hayden, 2003; IPCC, 2007). Abiotically, treeline shifts in altitude and latitude have corresponded to episodic events such as prolonged periods of warming temperatures, drought, or both, plus rising and falling CO_2 levels in the atmosphere. Anthropogenic impacts such as fire, agriculture, and grazing by domestic and other introduced animals have also altered treeline altitudes on a global scale (Seppä et al., 2002; Sarmiento & Frolich, 2002; Parmesan, 2006; Holtmeier & Broll, 2007). One important and fundamental question is whether current changes in global climate simply mirror paleo-historical patterns, or if they are unique (Williams & Jackson, 2007; IPCC, 2007). Despite the growing information on treeline shifts corresponding to derived macroclimate patterns, this paleological approach provides little detail about the actual ecophysiological mechanisms driving treeline altitudes.

Limiting Environmental Factors at High Altitude

Despite a growing data set, both paleological and contemporary data have not generated consistent conclusions about which specific environmental parameters are dictating the altitudes of treelines and, thus, the spatial distribution patterns of high-altitude forests (see Holtmeier & Broll, 2007; Weiser & Tuasz, 2007 for reviews). Moreover, field studies of the effects of enriched CO_2 and warmer temperatures on high altitude forests, as well as accompanying effects on water and soil nutrients, have involved only older life stages (Zak et al., 2000; Grace et al., 2002; Hättenschwiler et al., 2002; Millard et al., 2007). Similar studies on pre-establishment life stages at the upper limit of tree growth are comparatively rare. It is now recognized that more studies combining field measurements and experiments to evaluate the ecophysiological mechanisms of treeline altitudes are needed to supplement the more traditional approaches correlating single, mean environmental parameters (e.g. air or soil temperatures) with different treeline altitudes (see Körner, 2003a, b, for review; Shi et al., 2008). Some researchers have stated that this

traditional approach generates only simplistic scenarios that disguise the complexity of the treeline phenomenon without contributing to a better causal (functional) understanding (e.g. Holtmeier & Broll, 2007). However, correlating such environmental factors as mean seasonal air and soil temperatures with treeline altitudes (Alvarez-Uria & Körner, 2007; Körner, 2007), especially on a global scale, provides clues to the more mechanistic, causal mechanisms even for treeline migration. Albeit, the idea that a "true" thermal treeline exists on a biogeographic scale, and that local deviations should not confuse the issue by being designated as treelines (Körner, 2007), seems to avoid data that could contribute significantly to any comprehensive understanding of the causal mechanisms controlling treeline altitudes. In addition, the little-known impacts of extreme episodic events (Gutschick & BassririRad, 2003), which are predicted to increase in intensity and frequency under current scenarios of climate change (Goldenberg et al., 2001; Webster et al., 2005), need serious consideration. For example, the onset of more intense and longer-lasting droughts could certainly overshadow more gradual increases in CO_2 levels and air temperature that might also be masked within evaluations of mean environmental parameters (Stockton, 1984; Graumlich, 1991; Brodersen et al., 2006).

Another suggested approach for understanding treeline altitudes involves the development of more mechanistic vegetation models that include early pre-establishment life stages and corresponding microclimatic conditions as drivers (Wolf et al., 2008). Microclimatic factors associated with the pre-establishment process, plus the subsequent development of ecological facilitation as plant density and cover increase, need to be characterized for both summer and winter conditions in treeline ecotones (Choler et al., 2001; Smith et al., 2003). The potential influence of both ecological competition and facilitation (biotic and abiotic) within ecotones is a critical component for understanding the altitudinal boundaries of a subalpine forest in a changing environment (e.g. Choler et al., 2001; Zvereva & Kozlov, 2004; Michalet, 2006; Brooker et al., 2008). This general approach is fundamental to understanding distributional shifts and encroachments between virtually all contiguous plant communities (see review by Risser, 1995).

Does High Altitude Impact Carbon or Water Relations More?

Nearly all abiotic features of high altitude are most dependent on microsite/microclimate conditions, rather than altitude *per se*. However, there is one colligative property of increasing altitude that is not dependent on microsite—decreasing atmospheric pressure (e.g. Gale, 1972b). All other environmental factors associated with altitude may vary substantially with microsite conditions (e.g. sky exposure, air and soil temperature, humidity, wind, soil water and nutrients). Furthermore, two properties of mass diffusion in the gas phase are dependent on pressure and, thus, also change with altitude– an increase in the diffusion coefficients for mass diffusion rates (including CO_2 and water vapor) and changes in ambient concentrations (partial pressures; Fig. 1; Gale, 1972a, b, 1973, 2004; Smith & Geller, 1981). The decline in ambient CO_2 concentration with increasing altitude has been shown to be almost completely compensated by the more rapid diffusion of CO_2 molecules at lower pressure, with relatively slight decreases due to cooler air temperatures (Smith
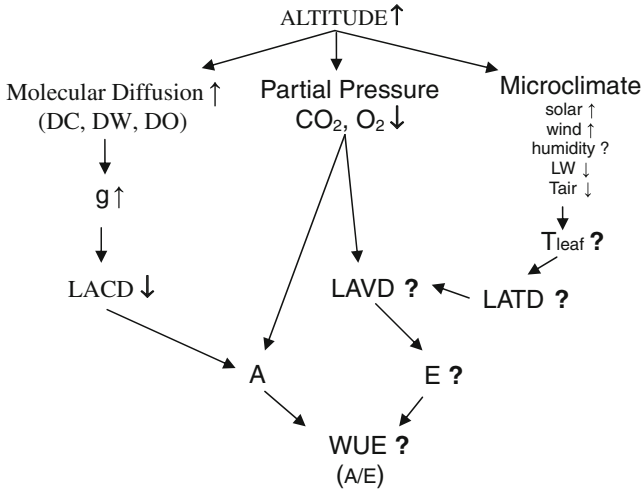
Fig. 1 Schematic representation of abiotic factors influencing photosynthetic gas exchange at high altitudes. More rapid mass diffusion at lower atmospheric pressure is the only inherent (colligative) property of increasing altitude, all others are microsite dependent. *Arrows* denote increasing or decreasing values with greater altitude; acronyms are as follows: *DC, DW, DO* are mass diffusion coefficients for CO_2, water vapor, and O_2, respectively; T_{leaf} is leaf temperature; LATD is the difference between leaf and air temperature; LAVD is the water vapor difference between the leaf and air; LACD is the leaf-to-air difference in CO_2 concentrations; A and E are photosynthesis and transpiration, respectively; WUE is the ratio A/E, water use efficiency. *Arrows* indicate where increases or decreases in the associated parameter are known. *Question marks* indicate unknown or variable responses according to geography and orographics (taken from Smith & Johnson, 2008). Figure 2 shows simulated changes in water use efficiency according to air temperature lapse rates and with hypothetical assumptions about several of the microclimatic parameters driving E

& Donahue, 1991; Terashima et al., 1995). As a result of a faster mass diffusion compensating for a lower ambient CO_2 concentration and, thus, smaller gradient (driving force) for diffusion, photosynthetic CO_2 uptake at higher altitudes appears similar to sea level values. However, some investigators still consider that photosynthetic CO_2 uptake is more difficult at higher altitudes (lower ambient pressure) because of lower ambient CO_2 concentrations (see review by Körner, 2003a, b). Changes in atmospheric water vapor concentrations with altitude are not as predictable because the sources of evapotranspiration (vegetative, soil, and free-standing) and corresponding temperature regimes are strongly interrelated in their generation of ambient water vapor concentrations (Smith & Geller, 1981).

Opposite to CO_2 uptake, plant transpiration with higher altitude is amplified by increasing mass diffusion rates of water vapor away from the leaf at any given degree of stomatal opening (Fig. 1). However, there is also a compensatory effect due to cooler air temperatures (especially higher lapse rates in air temperature) that act to decrease the leaf-to-air water vapor gradient. In addition, more intense sunlight levels on clear days at higher altitudes may drive leaf temperatures well above air temperature, increasing the leaf-to-air vapor gradient vapor gradient (Smith & Geller, 1981; Leuschner, 2000; Fig. 1). There is also a limited amount of data on changes in water vapor pressures (absolute humidity) with altitude, making computations of leaf-to-air vapor gradients impossible, along with corresponding predictions about

the effects of altitude on transpiration (Leuschner, 2000; Smith & Johnson, 2008). Regardless, computer simulations showed that transpiration increased most strongly with altitude for more humid mountains with low air temperature lapse rates, characteristic of coastal areas rather than drier continental regions (Fig. 2; Smith & Johnson, 2008). In contrast, computed water use efficiency (photosynthesis/ transpiration) increased for simulated drier mountains with higher lapse rates in air temperature, but decreased for higher humidity mountains (lower lapse rates).
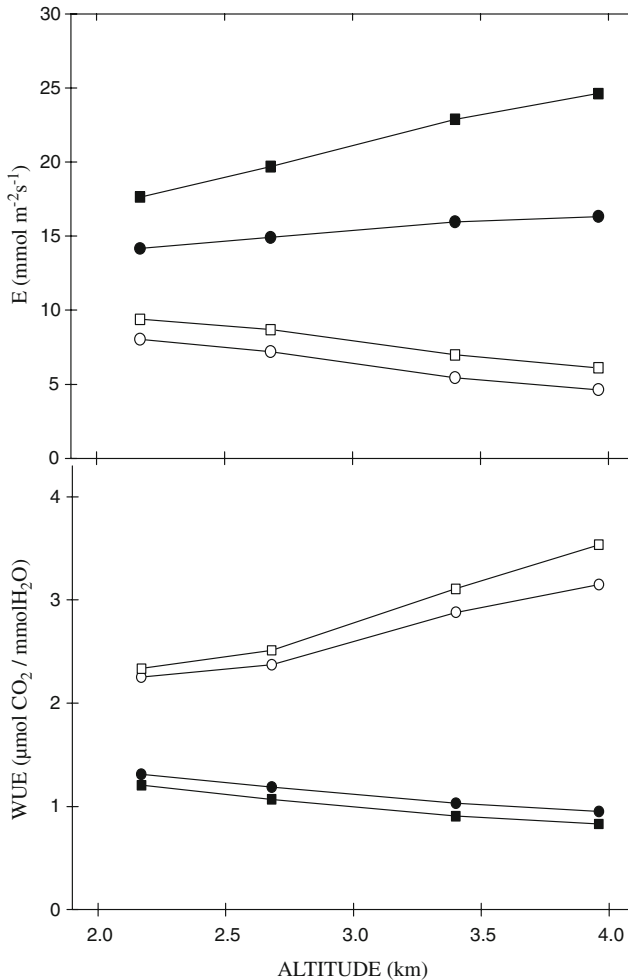

Fig. 2 Modeled and measured effects of increasing altitude on plant transpiration for mountains with contrasting lapse rates in air temperature (e.g. coastal versus continental mountains). (*a*) Simulated transpiration (E) with altitude computed as the product of LAVD and a constant g (400 mmol m^{-2} s^{-1}), or g proportional to a changing DW (as defined in Fig. 1). *Curves* represent wet lapse rate (−3.0°C/km) and constant g (*filled circle*), dry lapse rate (−8.0°C/km) and constant g (*empty circle*), wet lapse rate and g proportional to DW (*filled square*) and a dry lapse rate with g proportional to DW (*empty square*). (*b*) Simulated changes in water use efficiency (WUE) with altitude for the same conditions as in (*a*; modified from Smith & Johnson, 2008)

The increase in mass diffusion rates caused by decreasing ambient pressure with altitude, and a greater leaf warming by higher sunlight incidence, also points to the demand for greater water use efficiency (Fig. 2), or adaptations enhancing uptake of soil water, e.g. enhanced fine root systems, mycorrhizal associations, and investment in better plant hydraulics for water supply to leaves. This adaptive feature may be especially important for avoiding the catastrophic disruption of xylem hydraulics commonly associated with freeze-thaw episodes (e.g. cavitation) common to higher altitudes even during summer (e.g. Mayr et al., 2003, 2007). The hydraulic capabilities of the xylem are now recognized as a major constraint on plant water status and growth processes in mature life stages of a number of tree species (Sperry, 2000; Wullschleger et al., 2002; Niklas & Spatz, 2006; Niklas, 2007). Thus, the hypothesis that a limitation to carbon allocation to root growth due to cold soil temperatures (proposed for adult trees by Körner, 1998) could be an even more important factor in pre-established seedlings (little water storage capacity), possibly leading to a high mortality in treeline ecotones (Cui & Smith, 1990, 1991; Germino & Smith, 2001; Hasselquist et al., 2005). In this regard, the unchanging, or even increasing, amount of non-soluble (mobile) carbohydrates measured in adult trees at higher altitude has been considered evidence for the limitation of carbon acquisition versus processing at treeline (Körner, 2003b; Shi et al., 2008). In contrast, decreased photosynthetic carbon gain in pre-establishment seedlings has been associated with reduced root growth and accompanying mycorrhizal colonization, as well as a symptomatic death by desiccation (discussed in more detail below). In fact, there are data suggesting that mycorrhizal infection is initially parasitic and young seedlings may be preferentially selected for colonization based on high carbohydrate contents (Hasselquist et al., 2005; Kytöviita & Ruotsalainen, 2007). Moreover, if water-use efficiency lessens with altitude (Fig. 3), it can be assumed that nutrient-use efficiencies (e.g. nitrogen uptake per water lost or CO_2 gained) may also be lowered. A few reports have implicated water stress on carbon gain as limiting the altitude of a treeline via impacts on seedling survival (e.g. Smith et al., 2003; Geiger & Leuschner, 2004). However, it must be kept in mind that most environmental differences influencing plant water relations at any altitude are also dictated by microtopography and microsite characteristics (Friend & Woodward, 1990), although mass diffusion properties associated with altitude and lower ambient pressure are independent of microsite characteristics (Smith & Knapp, 1990). Thus, in contrast to altitude effects on photosynthetic CO_2 uptake, transpirational water loss and simulated water use efficiency can either decrease or increase with altitude depending on the mountain system (Figs. 2 and 3). Cold soil temperatures at high altitude and impacts on root growth, mycorrhizal infection, and plant water relations, even while above-ground tissues may be much warmer, have been suspected for some time as limiting annual carbon gain, e.g. spring and early summer (Smith & Knapp, 1990).

Limitations to Tree Establishment and Growth: Carbon Gain or Processing?

Although not yet considered for pre-established treeline seedlings, the question of carbon gain limitations versus limitations in the processing of assimilated carbon has entered the conceptual arena for understanding treeline altitudes (Körner, 1998,
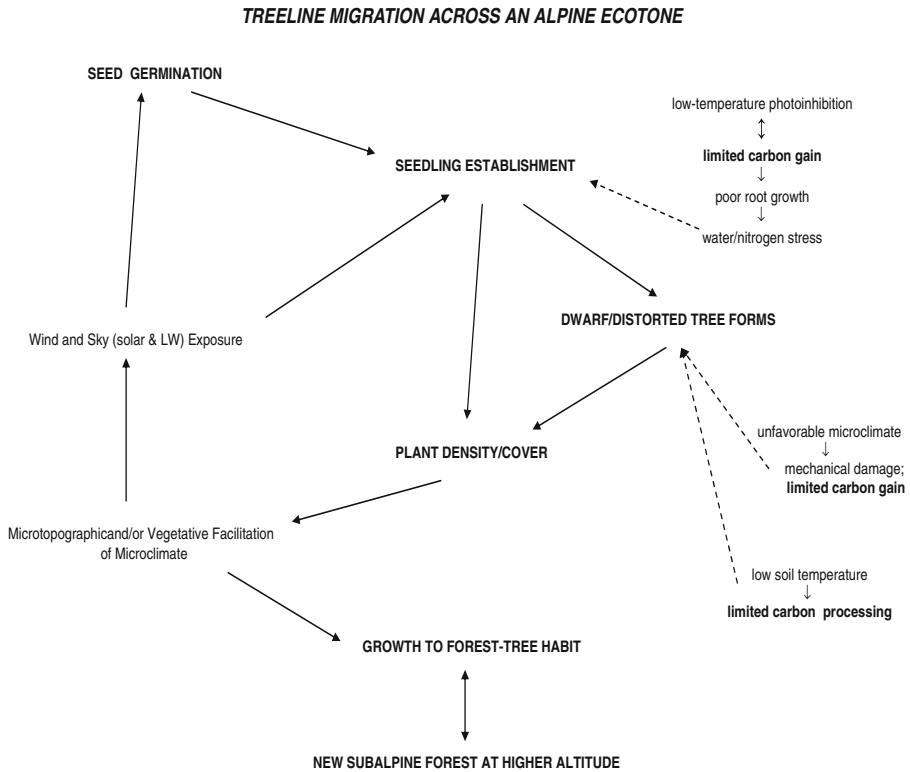
TREELINE MIGRATION ACROSS AN ALPINE ECOTONE

Fig. 3 Ecophysiological relationships proposed for the migration of a timberline/tree line to a higher altitude or, effectively, in determining the altitude of tree line. *Double-ended arrows* indicate a feed-forward and feed-back relationship between to processes. Carbon gain limitations have been proposed for establishing seedlings versus carbon processing limitations proposed for adult trees, while all life stages are influenced by ecological facilitation of microclimate. *LW* is long wave radiation from the sky at night. See text for further explanation

2005; Grace et al., 2002; Shi et al., 2006, 2008; Millard et al., 2007). Given that greater mass diffusion rates with altitude can compensate for lower concentrations of ambient CO_2, there is recent focus on the importance of carbon processing that contrasts sharply with the "carbon-centric" view that the altitude of treelines coincides with the limit of adequate annual carbon gain for survival (e.g. Tranquillini, 1979; Holtmeier, 2003). Experimental findings that show respiration to be more sensitive to warming than photosynthesis have also fueled this debate (Grace et al., 2002), along with studies showing that the level of non-structural carbohydrates does not decrease with higher altitude (e.g. Hoch et al., 2002). Instead of limitations in photosynthetic carbon gain, the respiratory-driven processes involved in processing assimilated carbon for repair and new growth may be limiting, and, thus, responsible for determining the altitudes of treelines across the globe. Another idea proposed is that photosynthetic carbon acquisition in tree species may be limiting only because nutrient uptake is curtailed by inadequate root growth (Millard et al., 2007). However, no increase in soil nitrogen contents, mineralization, or N_2 fixation rates have been found under elevated CO_2 regimes

(e.g. De Graaff et al., 2006). It has been proposed that nitrogen cycling is unlikely to keep pace with the measured increases in net productivity, creating an ultimate limitation due to nutrients (e.g. nitrogen) and not carbon acquisition (Millard et al., 2007). Also, a recent study addressing specifically the growth limitation hypothesis did not find evidence for carbon processing limitations, but rather carbon gain limitations in Himalayan trees at treeline (Li et al., 2008). Another recent study also tested the growth limitation hypothesis at treeline and reported no apparent sink limitation to photosynthetic carbon gain or growth at low temperatures in treeline trees (Susiluoto et al., 2007).

Recent reports have supported the idea that carbon acquisition (source/supply) is not limiting in tree species (e.g. Walsh et al., 1992) compared to the processing of assimilated carbon (sink limitations), i.e. the growth limitation hypothesis (Körner, 1998, 2003b; Grace et al., 2002; Shi et al., 2008). However, there is also a recent argument that assimilation of carbon can be considered limiting only if poor root growth limits nitrogen uptake (Millard et al., 2007). This nitrogen limitation hypothesis might also support the idea that limitation of root growth due to cold soil temperature is an environmental factor determining the altitudes of treelines (see Körner, 1998, 2003a, b for reviews). Thus, the high altitude inhibition of growth and the formation of a treeline could be determined by an inhibition of carbon processing at the root level, in line with the proposed ideas about nitrogen limitations due to inadequate root growth (Millard et al., 2007). However, these hypotheses have yet to be tested for the vulnerable, high mortality life stage of pre-establishment seedlings in treeline ecotones. Also, significant reductions in photosynthetic carbon gain in seedlings just older than the pre-establishment life stage (>3 years old) near timberline have been reported (Johnson et al., 2004; Brodersen et al., 2006; Johnson & Smith, 2007a, b), although limitations in carbon gain versus processing have not been differentiated.

A number of studies have reported initial increases in CO_2 assimilation rates in mature tree species growing experimentally under enriched ambient CO_2 levels (Hyvönen et al., 2007; IPCC, 2007). However, initial increases in carbon assimilation in several studies diminished to near or below pre-enrichment levels after a few years (e.g. Maurol et al., 1999). In addition, non-structural carbohydrates remained stable or increased with altitude in such high-altitude tree species as cembra pine (Hoch et al., 2002) and other shrub and tree species (Shi et al., 2006, 2008), and was assumed to be evidence that the processing of assimilated carbon was, not photosynthetic uptake. However, there are other tree species that have not shown increases in carbohydrate stores with altitude (Palacio et al., 2005), while other investigators have reported a strong correlation with the altitude of treelines and growth performance (e.g. Rathgeber et al., 2000). It has also been proposed that soil nutrient uptake, and not carbon acquisition or processing, may be the primary limitation to tree growth, notwithstanding inhibition of root growth and, thus, soil nitrogen uptake due to inadequate photosynthetic carbon acquisition (Millard et al., 2007). Supportive evidence for nitrogen limitations to tree growth comes from the carbon physiology of tree species, including the nitrogen binding capacity of the abundant carboxylation enzyme, Rubisco. However, nitrogen contents have been found to not increase with altitude (e.g. Shi et al., 2006).

Regardless of these suggested limitations to growth, little information exists that relates physiologically the non-structural carbohydrate or nitrogen levels in plant

tissues specifically to the balance between CO_2 uptake versus processing for growth. The fundamental question remains—does a changing carbohydrate level with altitude reflect carbon source (photosynthesis) versus sink (growth) limitations or, instead, a species specific trait for maintaining a constant carbon reserve, an attempt to alter carbon reserves depending on the stress level of the range, or even the simple result of low growth rates (e.g. Sveinbjörnsson, 2000)? This is a fundamental question that must be addressed before mobile carbon pools can be accepted as a functional indication of carbon source (acquisition) versus sink (growth) limitations (Sharkey et al., 2004). The idea that one core physiological pathway may be limited more than another core pathway, even though the two are tightly coupled by feed-forward and feed-back biochemistry, is an arguable concept. The highly conserved nature of these basic metabolic pathways in plants (e.g. photosynthesis and respiration) disputes the existence of an adaptive advantage of any physiological imbalance, even a temporary one (e.g., Williams, 1998; Sharkey et al., 2004). The close coupling between stomatal function and the hydraulics of water supply is another example of two primary processes that must be closely coupled for any adaptive advantage (Raven, 2002; Ainsworth & Rogers, 2007). Photosynthetic carbon supply (source) and carbon processing (sink) functions have also been found to be coupled evolutionarily at the species level, as is the case found for the similar biochemistry of C_4 and CAM species that evolved concentrating CO_2 mechanisms at the cell level (Osmond, 2007). Regardless of the possible existence of an imbalance between carbon gain and processing limitations at treeline, these ideas have yet to be tested for the high-mortality, pre-establishment life stages reported for treeline species at four different treelines (Cui & Smith, 1990, 1991; Germino & Smith, 2001; Geiger & Leuschner, 2004; Maher & Germino, 2006), as well as numerous other tree species from a variety of habitats (Harcombe, 1987).

Climate Change: Elevated CO_2 and Warmer Temperatures

The future of high-altitude forests must be considered in view of the documented, continuing trend in elevated CO_2 and warmer global temperatures, even though the effects of a host of associated changes in other environmental factors (such as precipitation patterns) could well be overriding. Some experimental data suggest that direct impacts of these two climate change parameters may have a secondary influence compared to such events as prolonged drought (e.g. Graumlich, 1991; Körner, 2003b), although these conclusions are, once again, drawn from studies on older, post-establishment trees and not from the generative life stages. The idea that growth and reproductive properties are typically more sensitive to warming temperatures than elevated CO_2 has also been proposed (Grace et al., 2002), with supporting evidence for rapid treeline advance coming from photographic and remotely-sensed data over the past few decades (Körner, 2005). However, data from experimental climate change studies (e.g. enriched CO_2 and warmer temperatures) have shown initial increases in carbon acquisition capabilities for growth in forest tree species, but a decline to pre-enriched levels after only a few consecutive years of enrichment (Hättenschwiler & Smith, 1999; Ainsworth & Long, 2005; Körner, 2006; Hyvönen et al., 2007; DeLucia et al., 2005). In

addition, although increased tree-ring widths in treeline trees have increased over the last 150 years (Paulsen et al., 2000), Nicolussi et al. (1995) concluded that elevated CO_2, not warming temperatures, was the cause. Handa et al. (2008) reported no increase in root growth after 4 years of enriched CO_2 for adult trees of treeline species in Switzerland.

Declines in reproductive effort have also been associated with enhanced carbon fixation and increased vegetative growth under enriched CO_2, e.g. alterations in flowering times (see review by Springer & Ward, 2007). In another study, Ward et al., (2000) reported that changes in flowering time under elevated CO_2 was the most important of all traits evaluated for influencing species fitness, even compared to enhanced biomass accumulation. Furthermore, flowering times under elevated CO_2 have varied among species, both phenotypically and genotypically (Springer & Ward, 2007). DeLucia et al. (2005) reported an increase in net primary production, but decrease in reproductive effort, in a loblolly pine stand enriched with CO_2 (FACE).

As discussed above, soil temperature and nitrogen abundance have also been implicated as potential environmental drivers of plant responses to climate change. One report concluded that any apparent CO_2 limitation to tree growth was the result of inadequate soil nitrogen uptake, which is needed to support the enhanced photosynthetic carbon gain because of restricted root growth (Millard et al., 2007), despite a large accumulation of ecosystem nitrogen (Finzi et al., 2006). Evidence for nitrogen limitations, as opposed to limitations in photosynthetic carbon gain, comes from other sources, e.g. the action of the photosynthetic Rubisco enzyme as a nitrogen source. Possibly, increases in nitrogen-use efficiency, and/or allocating more carbon to root growth and mycorrhizal requirements, could remedy this deficiency in nitrogen uptake capabilities under a future environment of greater atmospheric CO_2 (Finzi et al., 2006; Chapman et al., 2006). At the alpine treeline, limitations of cold soil temperatures to carbon processing and growth in adult trees has been proposed as causal to the formation of treeline at a particular altitude, as well as the idea that the large size of forest trees provide an important shading effect that contributes to cold soil temperatures and, thus, the altitude of a timberline (Körner, 1998, 2005; Shi et al., 2008). Inhibited photosynthetic carbon gain in new tree seedlings, leading to poor root growth, low mycorrhizal infection, and an apparent desiccation death, was also associated with high (often >95%) pre-establishment seedling mortality in a treeline ecotone in the Rocky Mountains, USA (Cui & Smith, 1991; Germino & Smith, 2001; Smith et al., 2003; Hasselquist et al., 2005; Germino et al., 2006; Maher & Germino, 2006). Although low soil nitrogen uptake could also be involved in this high mortality, none of these studies (or others to our knowledge) have evaluated experimentally the specific mechanistic impacts of elevated CO_2 and warmer temperatures on survival of pre-establishment life stages at treelines.

Study Priorities at Treeline: Mechanisms of Seedling Establishment and Growth to Forest-Tree Stature

Seedling establishment and subsequent growth after establishment are both necessary for the formation of new subalpine forest at higher altitude, and both appear to be particularly challenging for tree species in the upper treeline ecotone

(e.g. Smith et al., 2003; Fig. 3). The most apparent difference between trees and other species found at higher altitude is plant height, specifically a greater height above the ground that is accompanied by disfigurement in growth form (e.g. krummholz mats, flagging, and layering; see pictures in Arno, 1984). For ecotonal trees to grow tall, either away from the protective forest edge (timberline) or away from the protective boundary air layer next to the ground (generated both abiotically and biotically) they must tolerate or avoid higher wind speeds, a lack of winter snow coverage, plus increased sky (radiation) exposure during both night and day (Tranquillini, 1979; Hadley & Smith, 1987; Smith et al., 2003). While species of alpine plant communities are typically shorter in stature and more densely packed than their contiguous forest tree communities, most treeline conifer species show remarkable structural, phenotypic plasticity at several structural/ spatial scales, e.g. needle-like leaves, needle packing on shoots, tightly packed branches that form low-stature krummholz mats, and densely-packed tree islands (Smith et al., 2004). Spatially, as plant density and cover increase, important microclimate advantages in the treeline ecotone accrue, including enhancement of winter snow burial and summer microclimate advantages to establishing tree seedlings in the treeline ecotone (e.g. Smith et al., 2003; Fig. 4). For a subalpine forest to migrate into the treeline ecotone and, thus, to greater altitude the problem of tree height and the accompanying loss of protective microclimate appears to be paramount, extending from the germination life stage all the way to a new subalpine forest. In other words, the forest-like microclimate, or the forest itself, must exist before a tree with forest-like habit is possible (Figs. 3 and 4). Treeline ecotones with trees of forest-like stature are rare on a world scale (Arno, 1984).
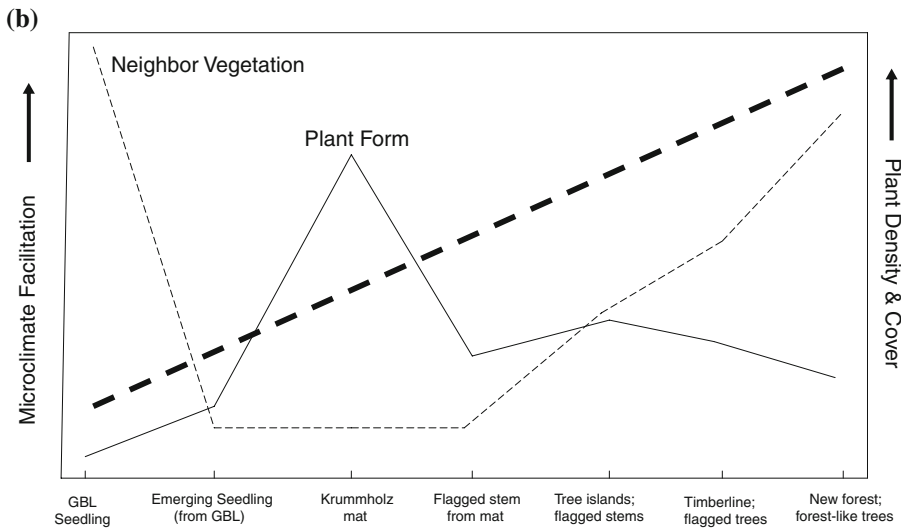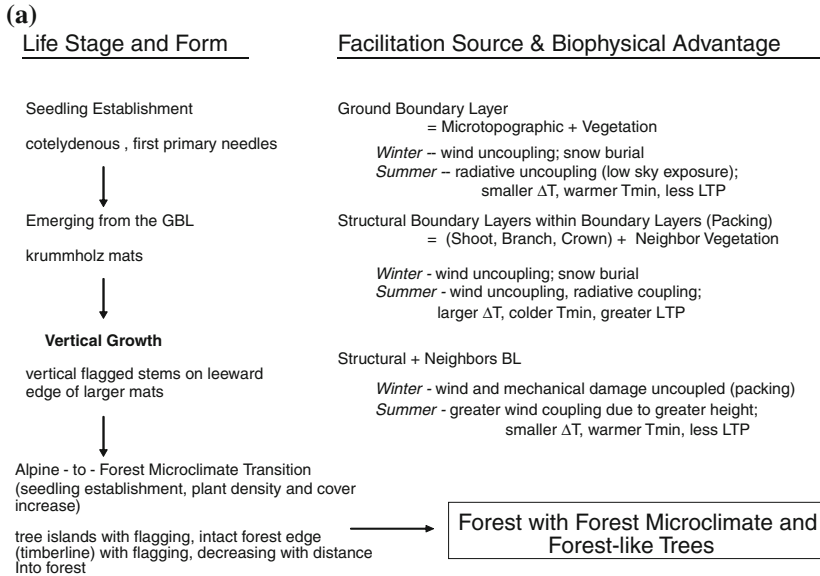
Seedling Establishment

Seed dispersal, germination, and seedling establishment within boundary ecotones must occur well in advance of any permanent changes in the spatial distribution pattern of mature forests (Noble, 1993; Smith et al., 2003; Zens & Peart, 2003). It is not that past or future studies on older life stages are not valuable, just not as proximal for understanding the distributional dynamics underway at treeline, and thus future changes in the distribution patterns of high-altitude forests. The long list of studies correlating mean abiotic variables (e.g. temperature isotherms) with the corresponding altitudes of treelines provide clues for evaluating the more mechanistic studies of the pre-establishment life stages. Although ideas about the environmental factors determining the upper treeline altitude have been proposed (e.g. Grace et al., 2002; Körner, 2005, 2007; Weiser & Tuasz, 2007), additional studies are needed to adequately address this complex question from a more mechanistic perspective (Smith et al., 2003; Holtmeier & Broll, 2007; Weiser, 2007a; Malanson et al., 2007). For example, the specific, functional role of vegetative and microtopographic facilitation involved in pre-establishment life stages at treeline has only recently been considered as an important mechanism for treeline migration (Hättenschwiler & Smith, 1999; Smith et al., 2003). Regardless of whether the physiology of carbon acquisition or processing, or water/nutrient uptake, is a primary limitation to growth and reproduction and will be more or less limiting in a warmer, CO_2-enriched climate, a new emphasis on the early generative life stages seems

warranted. As stated in Holtmeier and Broll (2007), "As to the functional 'mechanism' of treeline advance, studies on the functional relationships between regeneration success (survival of seedlings and saplings) are still comparatively rare in the treeline zones and are urgently needed". Compared to the abundance of studies on older tree life stages at treelines around the world, studies on pre-seedling establishment within boundary ecotones are rare (Risser, 1995). However, the importance of the pre-establishment life stages to understanding changes in spatial distribution patterns of high-altitude forests and treelines has been recognized recently (e.g. Geiger & Leuschner, 2004; Bader et al., 2007; Holtmeier & Broll, 2007; Weiser, 2007a). For example, Geiger and Leuschner (2004) concluded that the treeline altitude on a subtropical island was the result of multiple stresses on establishing seedlings, not adult trees. Also, the carbon sink-limitation hypothesis due to cold soils (proposed by Körner, 1998, 2003a, b) did not appear to be a factor in determining this treeline altitude—significant soil surface shading by trees, or the occurrence of stunted/ deformed trees were not observed. Similarly, establishing seedlings in treeline ecotones do not shade the soil surface to any extent and, thus, could not influence directly the altitude of timberlines and treelines via soil shading/cooling effects (Smith et al., 2003).

In the case of the alpine treeline ecotone, recent investigations involving pre-established tree seedlings found a high mortality (>90%) that was associated with excessive sunlight and nighttime sky exposure (low minimum temperatures), and soil water stress (Ball et al., 1991; Germino & Smith, 1999, 2001; Germino & Smith et al., 2002; Egerton et al., 2000; Maher et al., 2005; Maher & Germino, 2006). In contrast, some investigators have also suggested that the altitude of treelines does not serve as a sensitive indicator of rapid climate change compared to differences in the growth responses of forest trees just below treeline (Körner, 2003b), and according to dendrochonological evidence (e.g. Paulsen et al., 2000). Changes in new seedling occurrence from 1 year to the next can vary dramatically at treeline (Malanson, 1997), but some longer-term pattern in abundance might serve as an early signal of future changes in the distribution pattern of high-altitude forests. Smith et al. (2003), Holtmeier and Broll (2007), Weiser and Tuasz (2007), and Malanson et al. (2007) all conclude that these early life stages are a 'snapshot' of

(a)

Life Stage and Form	Facilitation Source & Biophysical Advantage

Seedling Establishment

cotelydenous , first primary needles

Ground Boundary Layer
= Microtopographic + Vegetation

Winter -- wind uncoupling; snow burial
Summer -- radiative uncoupling (low sky exposure);
smaller ΔT, warmer Tmin, less LTP

↓

Emerging from the GBL

krummholz mats

Structural Boundary Layers within Boundary Layers (Packing)
= (Shoot, Branch, Crown) + Neighbor Vegetation

Winter - wind uncoupling; snow burial
Summer - wind uncoupling, radiative coupling;
larger ΔT, colder Tmin, greater LTP

↓

Vertical Growth

vertical flagged stems on leeward
edge of larger mats

Structural + Neighbors BL

Winter - wind and mechanical damage uncoupled (packing)
Summer - greater wind coupling due to greater height;
smaller ΔT, warmer Tmin, less LTP

↓

Alpine - to - Forest Microclimate Transition
(seedling establishment, plant density and cover
increase)

tree islands with flagging, intact forest edge
(timberline) with flagging, decreasing with distance
Into forest   →

Forest with Forest Microclimate and Forest-like Trees

(b)

early treeline migration and can provide a more dynamic, as well as mechanistic, understanding of treeline shifts in response to climate change.

As already mentioned, low photosynthetic carbon gain, accompanied by low water potentials, wilting and needle discoloration, reduced root growth and low mycorrhizal infection, led to the hypothesis that desiccation could be the cause of the high (>90%) mortality in pre-establishment tree seedlings in a treeline ecotone of the Rocky Mountains, USA (Cui & Smith, 1991; Germino & Smith, 1999, 2001; Hasselquist et al., 2005; Germino et al., 2006). As is the case for most root uptake studies, the close coupling between water and nutrient uptake capabilities is difficult to separate as causative factors for growth or survival. However, an indirect test of

Table 1 Physiological Responses of Emergent Seedlings of *Picea engelmannii* to Colonization of Root Surfaces by the Alpine-White Complex of Ectomycorrhiza Fungi

	Photosynthesis (μmol CO_2 m^{-2} s^{-1})	Conductance (mol H_2O m^{-2} s^{-1})	F_v/F_m	Water potential (MPa)*
Natural colonization				
Colonized	8.4±2.2[b]	0.16±0.04[b]	0.65±0.02[c]	−0.75±0.13[c, d]
Un-colonized	9.7±2.1	0.18±0.04[b]	0.65±0.02[c]	−0.65±0.13[c, d]
T[a] (*df*)	-0.43 (12)[b]	−0.43 (12)	0.12 (22)	−0.52 (23)
Experimental colonization				
Colonized	4.3±1.0	0.06±0.02		0.99±0.08[e]
Un-colonized	4.5±1.2	0.07±0.02		−0.91±0.21[e]
T[a] (*df*)	0.15 (12)	0.26 (12)		0.37 (7)

Data Are for Seedlings that Emerged Naturally from Seed in the Forest Understory and Became Colonized Naturally ("Natural Colonization"), or not, by Mycorrhiza, and Seedlings at the Timberline Site in Hyphal Exclusion Boxes that Either Had Inocula Added, or Not ("Experimental Colonization")

F_v/F_m is an estimate of the optimum quantum yield, or maximum photosynthetic potential of photosystem II ($n=6$–13)

[a] T-tests indicated no significant differences in any parameter between colonized and un-colonized seedlings at $\alpha=0.05$ (from Maher & Germino, 2006)

[b] Forest only

[c] Forest and timberline sites combined

[d] Predawn

[e] Midday

the carbon acquisitioning versus processing limitation in treeline seedlings was reported in Germino et al. (2006; Table 1; Fig. 5). Figure 5 shows a positive association of fungal symbionts and successful tree seedling establishment, while Table 1 shows that there is no apparent physiological benefit for seedlings in a variety of measurable parameters that indicate various components of the photosynthetic processes. In microsites at timberline, where tree seedling photosynthesis and survival were substantially greater, tree seedling roots also had greater amounts of mycorrhizal fungi, although experimental manipulations of root fungi did not elicited strong physiological responses in host seedlings (Germino et al., 2006). In an earlier study, a positive association was found between infection by ectomycorrhizae and seedling establishment success, but the only positive benefit to seedlings appeared to be greater water status, with no apparent benefit to seedling photosynthesis or growth (Hasselquist et al., 2005). It is interesting that mycorrhizal infection and symbiosis is also known to be limited at a relatively high soil temperature (well above freezing) well above the proposed 5-8 C minimum for growing-season mean temperatures at treeline on a world scale (Körner, 1998, 2003a, b; Shi et al., 2008). These results suggest not only a strong positive association between fungal infection and successful establishment of treeline seedlings due to improved carbon gain, but that the fungal symbiont did not appear to benefit the seedling as much as the fungi was initially attracted to the establishing seedling due to increased seedling vigor (e.g. photosynthetic carbon gain). In
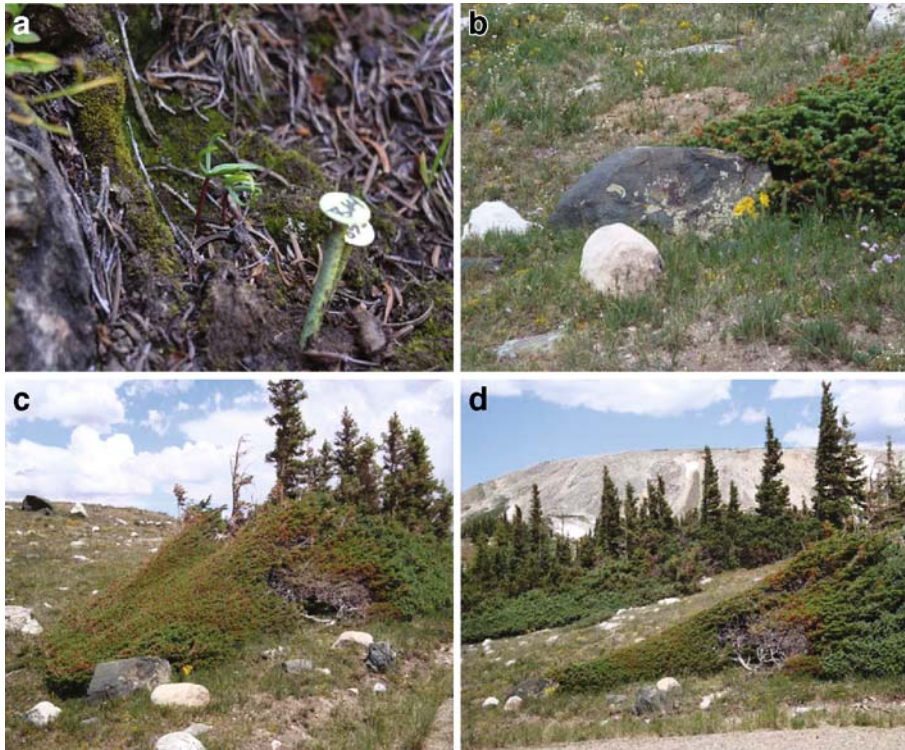
Fig. 5 Developmental chronology of new subalpine forest formation at a higher altitude. Facilitated (leeside of rock) seedling establishment (**a**, **b**), wind-driven krummholz mat formation (**b**), vertical shoot escape to form a flagged stem (more tree-like statue) at leeward sides of mats (**c**). Background in (**d**) shows the additional facilitation effects of multiple mats clustered together and the resulting increased escape of more shoots to form flagged trees. Ultimately, continued seedling establishment and the increased fusion of individual mats and flagged tree islands leads enable the formation of new subalpine forest at a higher altitude (i.e. new timberline/tree line altitudes)

addition, the advantages of microsite facilitation by surrounding vegetation outweighed the possible competitive impacts on water relations (Germino & Smith, 1999). Possibly, this initial vigor and attraction of mycorrhiza is a carbon gain limitation that will eventually be offset by fungal advantages to the seedling (Zak et al., 2000; Hasselquist et al., 2005; Germino et al., 2006). Few studies have measured pre-establishment seedling mortality at alpine treeline over any time scale (Bader et al., 2007; Gimenez-Benavides et al., 2007), although previous findings have been reported for other tree species and habitats (e.g. Harcombe, 1987; Boerner & Brinkman, 1996; Zens & Peart, 2003). Bader et al. (2007) and Gimenez-Benavides et al. (2007) provide a summary of investigations of these treelines and report a combination of fire effects and avoidance of high sunlight levels and low nighttime sky exposure (minimum nighttime temperatures) for dictating seedling establishment and survival above Andean timberlines. The upward movement of a treeline appears dependent on a considerable amount of ecological facilitation (both microtopographic and vegetative) of microclimate that begins with successful germination and is followed by the successful growth of new

seedlings to an undistorted tree, i.e. with forest-like stature (Egerton et al., 2000; Smith et al., 2003; Butler et al., 2004; Brooker et al., 2008).

Growth to a Forest-Statue Tree

For a subalpine forest to increase in altitude, vegetative facilitation of microclimate (without microtopographic facilitation) must continue to increase vertically to protect taller, established seedlings and saplings (Figs. 3 and 4). This protective, vegetative facilitation continues after establishment to uncouple individual trees from negative wind and radiation (solar and long wave at night) effects during both summer and winter, and increases as plant density and cover increase (Cui & Smith, 1991; Smith et al., 2003). An analogous uncoupling process can be seen across multiple structural and spatial scales (Gosz, 1993; Grace et al., 2002; Smith et al., 2004; Mori et al., 2008; Smith & Hughes, 2008) in the treeline ecotone (e.g. needle packing on sunlit stems, stem flagging, krummholz mats, tree islands, and the formation of ribbon forests) as distance from the timberline edge (i.e. exposure) increases (Smith & Carter, 1988; Smith & Brewer, 1994; Smith et al., 2003, 2004, 2008; Cairns, 2005; Mori et al., 2008). For example, the krummholz mat growth form is highly adaptive it that it enables early snow trapping and accumulation that buries needles, protecting them from severe winter damage and death (Hadley & Smith, 1987). Warmer needle temperatures, well above air temperature, are also generated during the day in summer. Furthermore, the occurrence of 'escaped' vertical stems only on the extreme downwind edge of larger krummholz mats is dynamically similar to the ultimate transformation of stunted/disfigured growth forms of ecotonal trees to the forest-tree habit characteristic of the intact subalpine forest. Even at the highest, most exposed locations in the treeline ecotone, larger krummholz mats will act to slow abrasive wind flow (frictional drag) at the leeward edge of the mat, allowing apical vegetative buds (but not leaves) to survive the abrasive boundary air layer of blowing ice crystals (Smith et al., 2003). Once the apical bud is above this lethal boundary layer blowing ice crystals, vegetative buds sprout and form new needles on branching stems. Initially, these vertical stems will remain flagged for the same reasons above, until neighboring trees increase in density and cover, providing protection from abrasive, wind-blown snow that can damage cuticles in drier continental climates as well as excessive snow deposition and stem breakage in areas where warmer temperatures generate wetter, heavier snow (e.g. more maritime mountain systems with strong oceanic influence).

Community Facilitation of Microclimate: Canopy Closure at the Landscape Level

In a manner dynamically similar to stem escape from abrasive boundary layer above the krummholz mat, initial seedling establishment and continued growth is prerequisite to increases in tree density and cover that culminates in new subalpine forest microclimate (Figs. 3 and 4). This process is evident within the spatial progression toward the timberline, beginning with the highest krummholz mats, followed by mats with leeward flagged stems, and finally tree islands larger and larger tree islands as the forest edge nears (see also Holtmeier & Broll, 2007). This gradual process results, ultimately, in the formation of a more forest-like

microclimate that is uncoupled from both summer and winter conditions. This uncoupling in plant temperatures from air temperatures was detectable as warmer mean canopy temperatures (infrared temperature measurement) during the day (Körner, 2007; Leuzinger & Korner, 2007), although not as warm as an adjacent alpine heathland that was even more uncoupled (i.e. shorter and more influenced by the ground boundary layer (e.g. Grace et al., 2002; Fig. 4). However, these warmer mean canopy temperatures measured thermally during the day can result from a potentially large variation between maximum temperatures of sunlit branches and minimum temperatures of shaded shoots in the canopy and, therefore, not reflect accurately actual leaf temperatures. In fact, it is possible that few or no leaves are at the mean canopy temperature measured, a common problem when interpreting canopy temperatures using infrared thermometry remotely. Importantly, this greater uncoupling from air temperature and warmer daytime needle temperatures due to packing also generates a greater coupling to the radiation environment and, thus, greater long wave cooling and lower minimum temperatures at night (e.g. Smith & Brewer, 1994; Jordan & Smith, 1995; Fig. 4). As discussed above, this large diurnal temperature swing for uncoupled plants (particularly the lower minimum temperatures) may also contribute to the severe low-temperature photoinhibition of photosynthesis and high mortality reported for sky-exposed, pre-establishment tree seedlings in treeline ecotones (Ball et al., 1991; Germino & Smith, 1999, 2001; Bader et al., 2007). In essence, some degree of both wind and radiative uncoupling is necessary for favorable microclimate conditions at high altitude. Uncoupling from wind can enhance such important features as snow deposition in winter, as well as daytime needle warming and lower minimum needle temperatures at night in summer, creating a larger diurnal change in needle temperatures (Jordan & Smith, 1995). It is significant that the inherent characteristic of tree species to grow tall will decrease the diurnal change in temperatures by lowering the daytime maximums and raising the nighttime minimum temperatures due to the greater wind speed as height above the ground increases (Fig. 4). Regardless, some degree of intact forest structure is needed before a favorable microclimate (especially during winter) will be generated so that greater seedling establishment can lead, ultimately, to trees with forest-like stature (Smith et al., 2003). This favorable, more forest-like microclimate appears to require, at least, protection from potentially severe wind damage (abrasion and loading) during winter, along with protection from sky exposure, both day and night, during the summer growth period, especially for pre-establishment seedlings but also for the subsequent vertical growth required to become a forest-like tree (Figs. 3 and 4). Other factors such as soil moisture and nutrients (e.g. snow collection leeward of established tree forms) could certainly play and important role as well (e.g. Hättenschwiler & Smith, 1999; Fig. 6).

Predicting Future Changes in High-Altitude Forests

Spatial boundaries between contiguous plant communities provide an opportunity to observe the early dynamics associated with changes in plant distribution patterns over a wide spectrum of spatial scales (Slatyer & Noble, 1992; Wiegand et al., 2006). In this regard, treelines represent the altitudinal limit of forest tree growth,
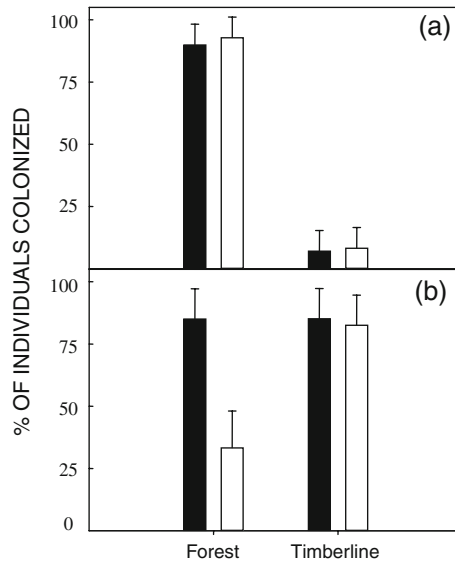
Fig. 6 Mean (±SE) percent of emergent (*a*) and juvenile (*b*) seedlings of *Abies lasiocarpa* (*solid*) and *Picea engelmannii* (*open*) colonized by the alpine white complex of fungi at the forest edge (timberline). Low infection rates at timberline compared to the adjacent forest understory, along with correspondingly low survival rates in newly emerged seedlings (<2 years old) at tree line, may indicate a carbon gain, root growth, water stress, and mortality interrelationship. New seedling occurrence diminished across the tree line ecotone until none were found at tree line (*n*=3 transects per site, with 83 emergent and 101 juvenile seedlings overall (modified from Germino et al., 2006)

forming a distinct transitional boundary (ecotone) between two remarkably different vegetation types, e.g. the subalpine forest and alpine communities composed of sub-shrubs, grasslands, and tundra. However, the long-lived nature of most treeline tree species results in sluggish changes in observable distribution patterns that are only discernable over at least decadal time frames. A central challenge will be to identify and measure parameters at treeline that will provide greater temporal resolution and are particularly responsive to the specific components of climate change. Thus, studies of the vulnerable, yet more dynamic, pre-establishment life stages (e.g. seed abundance, germination success, seedling establishment) in treeline ecotones may be especially revealing for understanding the mechanisms responsible for future treeline migration, e.g. the potential formation of new subalpine forest at a higher altitude under current climate change scenarios (Grabherr et al., 1994; Grace et al., 2002; Holtmeier & Broll, 2007; Weiser, 2007b)

Summary and Conclusions

As observed frequently, forest trees have increasing difficulty establishing and growing to the stature of a forest tree (e.g. krummholz and flagged tree forms) as distance from the intact subalpine forest edge (timberline) increases across the treeline ecotone. A fundamental mechanism driving the ultimate formation of new subalpine forest at higher altitude is the increased facilitation of microclimate that

occurs gradually with increasing tree density and cover. Progression toward a more forest-like microclimate (both summer and winter) depends initially on increased seedling establishment necessary for spatial closure among established trees. Limiting factors include cold temperatures, sky exposure (day and night), wind exposure, air humidity, and a number of possible soil factors. The degree of biophysical coupling with wind and radiation exposure appears fundamental to this transformation in microclimate. Understanding the abiotic and biotic factors associated with this ecotonal process will enable more accurate predictions about the response of high-altitude forests to climate change.

The occurrence of insect and disease outbreaks associated with current scenarios of climate change could also be critical to the future character of high-altitude forests (e.g. Dale et al., 2001; DeLucia et al., 2008). As discussed further below, changes in cloud patterns could have particularly rapid and strong impacts on all aspects of high-altitude ecosystems, especially annual water dynamics of large geographic regions (Stanhill & Cohen, 2001; Andrews & Foster, 2008; Gregory & Webb, 2008).

Despite paleological reconstructions of past altitudinal shifts and expansions/ contractions in the distribution of high-altitude forests, corresponding information of past climate change, and more recent observations of altitudinal increases in alpine treelines of the northern hemisphere, predictions about the future distribution patterns of high-altitude forests remain tenuous. Even though accumulating data from climate change experiments on a number of forest tree species (e.g. FACE studies) has generated some interesting and unexpected observations, only speculative conclusions about future effects on high-altitude forests are possible (Hyvönen et al., 2007). Recent reviews of the causes of upper altitudinal limits of tree occurrence lists six current hypotheses: climatic stress, disturbance, insufficient carbon balance, limitation to cell growth and tissue formation, limited nutrient supply, and limited regeneration (e.g. Körner, 2003a; Weiser & Tuasz, 2007). To our knowledge, none of these hypotheses are based on research related to pre-establishment life stages of tree species in the treeline ecotone, a prerequisite first-step in treeline migration. Information about the specific effects of climate change on pre-establishment life stages, and accompanying increasers in facilitative plant cover, may or may not correlate with the extensive findings on adult tree productivity and growth at treeline. If root factors are implicated as dominant limitations, changes in the occurrence of drought episodes and impacts on soil temperatures and dryness need to be better understood. Elevated CO_2 and temperature impacts on root/ mycorrhizal growth and water/nutrient uptake may also be critical limiting factors for more mature life stages, although more comprehensive studies are certainly needed. The vascular transport of water (thus nutrients) absorbed from the soil could also be a limiting process that couples photosynthetic carbon gain and the growth processes supported directly by respiration. Specifically, information is needed concerning the influence of the vascular transport properties in pre-established seedlings with typically high mortality in treeline ecotones.

Cloudiness is also an important environmental parameter with a strong potential for altering a host of plant responses at high altitudes, e.g. the seedling water stress and low temperature photoinhibition of photosynthesis discussed above. The importance of sunlight and nighttime sky exposure (long wave radiation sink) to pre-establishment seedling survival (e.g. Johnson & Smith, 2007b; Reinhardt &

Smith, 2007) may also be particularly relevant because of recent reports of the rapid and strong impacts of climate warming on cloud cover (Gregory & Webb, 2008, Andrews & Foster, 2008), which could reduce incident sunlight levels, as well as the minimum temperatures at night due to greater long wave radiation from the sky.

An approach for understanding the integrative influence of soil water/nutrients, as well as carbon gain versus processing limitations, would be an investigation of relative growth partitioning in response to temperature and nutrient availability (e.g. Lambers & Poorter, 1992, Loveys et al., 2002). Future CO_2 enrichment and warming experiments, along with associated changes in water and nutrient regimes, could be a valuable experimental approach for resolving the relative importance of ecological facilitation to treeline migration. The importance of microclimate facilitation (from both abiotic and biotic sources), as well as competition, during pre-establishment life stages, plus the subsequent vertical growth away from the protective ground layer, needs further investigation. The future rate of expansion, contraction, and altitudinal migration of high-altitude forest boundaries will be strongly influenced by the mechanics of these two processes within treeline ecotones (Bekker et al., 2001; Bekker, 2005). There have been recent observations of severe biotic (parasite) damage to adult trees in the western USA (and elsewhere) that may be related to the impacts of a long-term drought. Thus, additional studies are needed to identify and evaluate possible "bottlenecks" to the generative/regenerative potential of alpine treelines that may be extreme and episodic, including, drought, fire, and parasite outbreaks, related either directly or indirectly to climate change.

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