

# Another perspective on altitudinal limits of alpine timberlines<sup>†</sup>

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**Summary** Recent hypotheses of timberline causation include the possibility that limitations to growth processes may be more limiting than restrictions on photosynthetic carbon gain, and that cold soil is a primary limiting factor at high altitude. However, almost all of the supporting data for timberline causation have come from studies on older trees, with little focus on the mechanisms of seedling establishment and the growth of saplings away from the forest edge into the treeline ecotone. We describe a conceptual model of timberline migration that invokes a strong dependence on ecological facilitation, beginning with seed germination and continuing through seedling establishment and sapling growth to the stage where trees with forest-like stature form new subalpine forest at a higher altitude. In addition to protection from severe mechanical damage, facilitation of photosynthetic carbon gain and carbon processing is enhanced by plasticity in plant form and microsite preference, enabling seedling survival and sapling growth inside and through the often severe boundary layer just above the ground cover. Several forms of facilitation (inanimate, interspecific, intraspecific and structural) result in substantial increases in photosynthetic carbon gain throughout the summer growth period, leading to enhanced root growth, subsequent amelioration of drought stress, and increased seedling survival. Avoidance of low temperatures and low-temperature photoinhibition of photosynthesis may be major benefits of the facilitation, enhancing photosynthetic carbon gain and respiratory-driven growth processes. We propose that the growth of vertical stems (flagged tree forms) from krummholz mats is analogous functionally to the facilitated growth of a seedling/sapling in and away from ground cover. Increasing abundance and growth of newly established trees in the treeline ecotone generates a structural and microsite facilitation characteristic of the subalpine forest below. This is followed by the formation of new subalpine forest with forest-like trees, and a new timberline at higher altitude.

*Keywords:* altitude, ecological facilitation, flagged trees, growth limitation, krummholz, photosynthesis, sapling growth, seedling establishment, treeline, water relations.

## Introduction

For more than a century, the question of why forest trees are not found above certain altitudinal limits has remained unanswered. The question is particularly relevant today because of the potential sensitivity of the limit to climate change (Moir et al. 1999, Jobbagy and Jackson 2000, Paulsen et al. 2000, Rupp et al. 2001, Grace et al. 2002). In particular, the possible loss of alpine species as a result of the upward encroachment of subalpine forest under a global warming regime is an important concern (e.g., Messerli and Ives 1997, Luckman and Kavanagh 2000).

In the broadest sense, an upper “timberline” is the highest elevation at which trees occur with a stature characteristic of trees found within the contiguous subalpine forest (Figure 1). In comparison, trees growing above this elevational limit are usually distorted structurally (e.g., krummholz mats, flagged, and stunted tree forms) and occur in diminishing numbers across a transitional region (ecotone) extending from the forest edge into the alpine tundra (Tranquillini 1979, Arno and Hammerly 1990, Stevens and Fox 1991, Körner 1999, Sveinbjornsson 2000). Likewise, the upper altitude limit above which trees no longer occur, even in severely stunted forms, is considered here to be the “treeline,” although a definition of treeline based on minimum tree height has also been used (e.g., Körner 1998). Between the timberline and treeline, the transitional ecotone may vary in width from tens to hundreds of meters, depending on the steepness of the gradient in biophysical and physicochemical factors. These altitudinal limits may also vary locally depending on wind exposure and the altitude of the perennial snowpack. Although seedling age and size vary greatly at timberline, the term seedling is used for trees 0–10 years old and the term sapling for trees older than about 10 years, but not sexually mature (e.g., cone forming). To understand the upper altitudinal limits of a particular timberline, the interactions of both abiotic and biotic factors must be considered. Abiotically, microsite and growth form differences that modify microclimate could raise the maximum altitude at which a particular tree might survive, and advance the

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Figure 1. Photographs of the basic facilitation processes involved in sapling growth at the alpine treeline ecotone in the Snowy Range of southeastern Wyoming, USA. (Top panel) Needle mortality caused by snow abrasion, and desiccation of vertical leaders that extend above the snow surface (living shoots beneath snow cover have green needles). (Middle panel) Dead (brown) needles on vertical leaders shown after snow melt in early summer. (Bottom panel) Survival of vertical leaders from the leeward edge of krummholz mats that will become flagged trees (apical buds may survive on leaders with dead needles at leeward edge of mat).

well-documented benefits of ecological facilitation over the negative impacts of competition (e.g., Egerton et al. 2000, Choler et al. 2001). A species microsite preference during the germination phase, structural facilitation from growth form modification, intraspecific and interspecific microsite facilitation,

life history, and physiological tolerance probably dictate establishment success in the treeline ecotone, as well as other boundary systems. Only abiotic factors influencing the upward migration of a timberline will be considered here. In addition, timberlines limited to a specific upper altitude primarily because of the steepness of the slope and absence of soil are excluded from this discussion.

### Review of recent hypotheses of timberline causation

Numerous studies have focused on correlative relationships between timberline altitudes and specific environmental parameters such as mean annual minimum temperatures. Körner (1998, 1999, 2003) has summarized the primary environmental factors implicated in determining the high-altitude limits of an alpine timberline and two new explanations for the altitudinal occurrence of upper treelines, based on annual mean temperatures (Table 1).

One explanation of timberline causation is that timberline conifers and other alpine species are unable to use the carbon gained from daytime photosynthesis in growth (growth limitation hypothesis) because of low soil temperatures. A variety of studies have been cited as evidence that growth limitation dictates the altitudinal occurrence of treelines. For example, the finding that stored carbon (sugars, starch, lipids) and leaf nitrogen concentrations are higher in conifers at the treeline than at lower altitudes (Körner 1998, Hoch et al. 2002, Hoch and Körner 2003) has been interpreted as evidence that carbon gain is less limiting than its use for growth at the treeline. However, this interpretation ignores the possibility that greater carbon storage is an adaptive characteristic of plants growing in stressful environments (cf. Chapin et al. 1990 for review). The observation that timberlines occur at locations with similar seasonal mean temperatures, but with  $\text{CO}_2$  partial pressures ranging from 55 to 94% of sea level values (Körner 1998), appears to refute the growth limitation hypothesis; however, the compensating effects of low pressure on increased diffusion rates were not discussed (Gale 1972, Smith and Geller 1981, Smith and Donahue 1991, Terashima et al. 1995). Tranquillini (1979) observed dramatic reductions in growth rates of treeline trees across a 200–300 m altitudinal gradient, even though solar radiation, season length, and carbon gain do not change appreciably across such a narrow gradient. Loris (1981) reported decreases in growth increment when temperatures fell below 5 °C, while photosynthetic rates remained between 25 and 60% of former rates. Körner (1998) concluded that the sink-oriented, growth-limitation hypothesis of treeline formation offers a better explanation for the doubling of tree ring width over a 2–3 °C warmer season (Mikola 1962, Schweingruber et al. 1988, Grace and Norton 1990). Recently, Hoch et al. (2002) reported that, across a tree ecotone, treeline sink activity (carbon processing for growth) appeared to be more restricted at higher altitude, but carbon gain did not change with increasing altitude, although starch and lipids were more plentiful in tissues of trees found higher in the ecotone. Grace et al. (2002) proposed that photosynthesis was

Table 1. Factors identified as important for understanding the altitudinal limits of upper timberlines worldwide, including five hypotheses recently reviewed by Körner (1998).

Hypothesis	Factors
1. Seedling and sapling establishment	Seed germination, growth and survival
2. Mechanical damage	Wind abrasion of needle cuticles, apical bud damage, snow loading and frost heaving cause tissue and whole-tree mortality
3. Physiological tissue damage	Low temperature and desiccation limits growth and survival
4. Annual carbon balance	Photosynthetic carbon gain minus respiratory demands is less than required for successful growth and reproduction
5. Biosynthesis and growth limitation <sup>1</sup>	Low temperature limitation on growth processes greater than on photosynthetic carbon gain

<sup>1</sup> Cold soil as a result of the large size of conifer trees and consequent soil shading has been hypothesized as a factor limiting the altitude of alpine treelines.

less temperature-sensitive than growth and reproductive processes, leading them to predict a rapid advance of the treeline with climate warming. They noted, however, that experimental data were needed to distinguish between photosynthesis and growth processes. Körner (2003) has proposed that tree growth on a global scale may not increase in response to continuing increases in atmospheric CO<sub>2</sub> concentration, because values of stored carbon pools remain relatively constant for tree species from contrasting biomes, even during periods of high vegetative growth or fruit production.

In contrast to the evidence supporting the proposed growth limitation hypothesis, the observed increased growth and improved carbon balance in high-elevation conifer trees in Switzerland (2180 m altitude) after exposure to elevated CO<sub>2</sub> concentration (Hättenschwiler et al. 2002) suggests that photosynthetic carbon gain is a strong limiting factor in these trees. Both maximum photosynthesis and non-soluble carbohydrates were greater after exposure to high CO<sub>2</sub> concentrations. Also, amelioration of temperature by the microclimatic facilitation processes illustrated in Figure 2 could influence both daytime and nighttime microclimate, and thus both photosynthesis and respiration-driven growth processes.

A second hypothesis of timberline causation states that the timberline, as well as the stunted growth of ecotonal trees, is due to inhibition of root growth (Körner 1998). It was suggested that the inhibition was a result of large conifer trees preventing sunlight penetrating and warming the soil (Table 1). Comparisons of soil temperatures in forests with adjacent grasslands or tundra (Wardle 1968, Munn et al. 1978, Körner et al. 1986), and observations of prolonged snow accumulation in high-elevation forests compared to tundra (Tranquillini 1979), are cited as support for this hypothesis. However, minimum air temperatures at ground level are reported to be highest when sheltered from night skies at the treeline and elsewhere (e.g., Leuning and Cremer 1988, Jordan and Smith 1994). Tree seedling establishment at the treeline is reported to be associated with proximity to larger tree forms and shading from the cold night sky and sunlight (Ball 1994, Hättenschwiler and Smith 1999, Germino and Smith 2002), as well

as with the understory of the adjacent, subalpine forest (Cui and Smith 1991). Ball (1994) reported the occurrence of tree-line seedlings (*Eucalyptus* spp.) only in areas beneath trees where both daytime and nighttime shade overlapped, indicating the potential importance of low-temperature photoinhibition of photosynthesis to seedling survival. Similarly, it has been shown that root growth is inhibited in cold soils (Bilan 1967, Tranquillini 1979, Häsler et al. 1999), as is photosynthesis (Day et al. 1990). Karlsson and Weih (2001) reported no relationship between soil temperatures and treeline sites with and without birch trees in northern Sweden, and Malanson et al. (2001) reported no correlation between soil resource patterns and the observed plant distribution pattern. Shading of soils by large trees does not appear to be relevant to the question of seedling establishment away from the timberline edge, where little self-shading occurs and exposed, sunlit soils tend to be warmer than in the forest understory (Hadley and Smith 1986). Thus, without additional evidence, the idea that soil temperature limits growth processes more than photosynthetic carbon gain seems tenuous.

### Alternative hypotheses

Nearly all studies of timberline causation have focused on factors influencing older trees at timberline and have provided little information on the specific mechanisms involved in the formation of new subalpine forest above the subalpine forest boundary. Moreover, the existence of older tree seedlings and saplings in treeline ecotones at many locations worldwide (e.g., LaMarche and Mooney 1972, Innes 1991, Rochefort et al. 1994) has been cited as evidence that seedling establishment is not a ubiquitous determinant of timberline elevation. Körner (1998) suggested that seedling emergence from the warmer boundary layer near the ground, or within a shrubby ground cover, was an important stage that limited the advancement of upper timberlines at many locations around the world (cf. Grace and Norton 1990, Stevens and Fox 1991, Ball et al. 1997). However, any advance of a treeline would require seedling survival above the current treeline elevation. According to



**MICROSITE FACILITATION AT ALPINE TIMBERLINE:  
Sky and Wind Exposure**

**SOURCE**

Inanimate (rocks, microtopography), structural (growth form), intraspecific (neighbors) and interspecific (neighbors)

**BENEFITS**Winter

Snow burial— prevents ice crystal abrasion and desiccation; warmer and less extreme diurnal temperature differences; no excessive sunlight exposure

Clustering at the shoot-to-landscape scale— increased snow deposition and burial

Flagging— prevents damage from snow loading and rime ice accumulation

Summer

Less sky exposure—

*Day:* less sunlight and lower temperatures

*Night:* higher minimum temperatures and less LTP; less dew and frost accumulation

Less wind exposure— warmer needles in sun

**POSSIBLE ADAPTIVE TRADE-OFFS**

Less sun and sky exposure due to burial and mutual shading—

*Day:* less sunlight and lower temperatures for photosynthesis

Less wind exposure—

*Day:* higher temperatures and greater transpiration

*Night:* lower minimum temperatures

Figure 2. Microsite facilitation at alpine timberline. Interactive factors leading to the facilitation involved in tree seedling establishment and sapling growth in the alpine treeline ecotone. Inanimate, intraspecific, interspecific, and structural facilitation can result in protective snow burial, as well as amelioration of subsequent growth limitation factors within and just above associated ground cover. Refer to text and Figure 4 for more detailed explanation and specific citations. Abbreviation: LTP = low-temperature photoinhibition of photosynthesis.

Körner (1998), the question is why seedling populations above the treeline do not develop into forest, but remain nested in the graminoid or shrubby ground cover or form crippled shrub. Our purpose in the following sections of this paper is to provide a more mechanistic, step-wise analysis of timberline/treeline migration to a higher altitude by identifying and evaluating the important abiotic factors limiting the successful establishment of seedlings and the growth of saplings to forest-tree stature.

The mechanisms involved in the upward migration of timberline to higher altitude must initially depend on new seedling establishment above the existing timberline, into the treeline ecotone. As proposed here, greater seedling/sapling abundance also provides the ultimate facilitation required for continued growth to full forest-tree stature, and the formation of new subalpine forest at higher altitudes. At high elevations, this migration of the timberline is possible only with the protective, mutual facilitation provided by neighboring trees and surroundings, similar to that found within the intact subalpine forest. In the Rocky Mountains of southeastern Wyoming, USA, the establishment of new tree seedlings into a treeline ecotone appears to involve considerable microsite facilitation by either inanimate objects (e.g., rocks, fallen logs) or intraspecific and interspecific associations (Germino and Smith 1999, 2000b, 2002). Structural self-facilitation (e.g., cotyledon orientation and primary needle clustering, krummholz mats) may also enhance seedling carbon gain and survival of seedlings and saplings (Figure 3). Increased seedling establishment and abundance is followed by even greater facilitation, leading to greater seedling establishment and sapling growth, thereby resulting in a positive feedback cycle. Thus, increased seedling/sapling abundance leads to the same shel-

tering effect that is necessary for the formation of the forest outposts, or islands, described by Schönenberger (2001) and referred to by Körner (1998) as potential shelters for improved seedling establishment. In addition, we propose that the ultimate development into a forest tree (undistorted growth form) is analogous functionally to the biophysical escape of vertical stems from the surface boundary layer of a krummholz mat (Figure 1 top panel). Subsequently, continued facilitation of the sapling stage is required to a degree approaching that found within the intact subalpine forest at lower elevation.

#### **Mechanisms of seedling and stem escape from vegetative ground cover**

Some of the most extreme timberline/treeline conditions may occur in dry continental mountains of temperate latitudes (e.g., Rocky Mountains, USA) where extremely low winter temperatures generate powder-like snow composed of abrasive ice crystals (Hadley and Smith 1983, 1986). As well, subfreezing temperatures at night persist throughout the summer growth period (Jordan and Smith 1994). In winter, ice crystals blown by the boundary air layer next to the snow surface can produce severe leaf cuticle abrasion. This phenomenon impacts any exposed leaves of evergreen species. Needle death due to desiccation has been documented for timberline/treeline conifers (Hadley and Smith 1986, 1987, 1989, 1990). Desiccation during inadequate snow cover has also been reported for the evergreen *Rhododendron ferrugineum* L. at the alpine timberline in Austria (Neuner et al. 1999). During a relatively short period in late spring and early summer, dead (brown) needles occur on the vertical leaders (previous summer's growth) that were not buried beneath the snow layer entrapped within

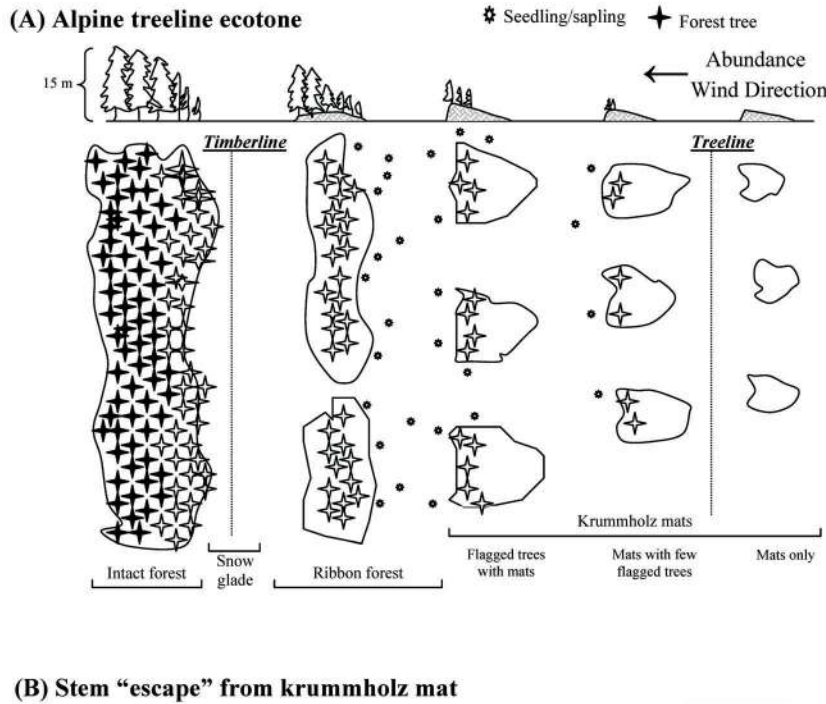


Figure 3. (A) Schematic landscape of the treeline ecotone and (B) cross-sectional schematic of a single krummholz mat with flagged trees at its leeward edge. Open symbols in (A) indicate flagged trees. In (B), dark area is the krummholz mat, overlying clear area is snowpack, and grey area is zone with high cuticle abrasion caused by a high concentration of blowing ice crystals, as well as greater sky exposure, lower minimum nighttime temperatures, high sunlight exposure (snow albedo), and possible herbivory. See text and Figure 1 for details of the functional analogy between seedling/sapling growth from the protective ground cover layer and the growth of vertical leaders from the surface of a krummholz mat to form flagged trees.

krummholz mat canopies (Figure 1 middle panel). Thus, needles on exposed shoots at the snow surface are pruned naturally, shaping the familiar conical mat that tapers away from the prevailing wind direction (Figures 1 and 3). In response to this pruning of apical meristems, lateral shoot development is promoted, leading to a dense (LAI > 20) leaf canopy that collects snow effectively during the first snow in early fall (Hadley and Smith 1987). As a result, all lateral shoots developed during the previous summer become buried beneath captured snow and survive the severe mechanical forces of high winds and abrasion characteristic of winter. Other factors such as herbivory by birds and small mammals may also contribute to the high mortality in new vertical shoots (S. Hättenschwiler, University of Basel, personal communication).

In the central Rocky Mountains, USA, established seedlings grow into krummholz mats that are composed of one or both of the dominant treeline conifers (*Abies lasiocarpa* (Hook.) Nutt. and *Picea engelmannii* Parry ex Engelm.). Efficient snow capture by krummholz mats is recognized as a structural self-fa-

cilitation that is critical for needle and shoot survival during winter, and results in higher needle temperatures and photosynthetic rates in spring and summer (Figure 1 top panel, Hadley and Smith 1987, Boyce and Lucero 1999). Survival of the apical bud on a single vertical shoot, while growing through the abrasive boundary layer at the snow-laden surface of a krummholz mat, is necessary for the escape of upright stems to form a flagged tree (Figure 1 top panel). Thus, both snow burial and growth through the boundary layer next to the snow surface are necessary for the formation of a flagged tree, which occurs first at the downwind edge of a krummholz mat (Figure 1). We propose that the survival of the apical bud on a vertical leader and its eventual development into a flagged stem above a krummholz mat is analogous functionally to the growth of a new tree seedling/sapling from other forms of treeline ground cover (e.g., grass, herbs and shrubs). Even for timberline areas without blowing snow and ice crystal abrasion, a host of abiotic factors make survival within, and escape from, the protective ground cover difficult and may involve

damage from frost, snow loading and rime ice deposition seasonally, if not daily (Holroyd 1970, Wardle 1974, 1977, Arno and Hammerly 1990, Messerli and Ives 1997). These stress factors not only inflict mechanical damage on shoots, but also limit photosynthetic carbon gain and growth of both seedlings and saplings inside and above the ground cover boundary layer.

### Growth through ground cover—seedlings and saplings

In addition to ice crystal abrasion, the boundary layer reduction in wind for young seedlings or saplings growing within or just above ground cover can result in especially low nighttime temperatures and high daytime temperatures, depending on the amount of sky exposure. With reduced sky exposure the lower daytime and higher nighttime temperatures can dramatically increase tree seedling survival in the timberline ecotone (Ball 1994, Germino and Smith 1999, 2000b). These conditions also increase photosynthetic carbon gain and produce corresponding increases in root growth, mycorrhizal infection and survival in understory conifer seedlings growing naturally in microsites with either too much or too little sunlight (Cui and Smith 1991). In contrast, low photosynthesis and xylem water potentials are associated with increased sky exposure, leading to high mortality rates in treeline seedlings of the same species (Germino and Smith 1999). Specifically, low-temperature photoinhibition of photosynthesis occurs because greater sky exposure (day and night) results in reduced carbon gain and a correspondingly high mortality (> 90%) in conifer treeline seedlings (Germino and Smith 1999, 2002). More favorable microsites with lower sky exposure are also associated with higher water potentials and survival of seedlings, as well as avoidance of particularly low minimum temperatures at night and high incident sunlight the following day. Previously sky-exposed conifer needles on the surface of krummholz mats had maximum daytime needle temperatures more than 10 °C higher than the maximum air temperature, whereas minimum nighttime temperatures were more than 7 °C below the minimum air temperature (Hadley and Smith 1987). The lowest leaf and air temperatures (often near or below freezing at high elevation even in summer) were due to high rates of longwave radiation exchange with the cold night sky (cf. Jordan and Smith 1994). Cold air drainage and settling from elevated surroundings frequently lead to minimum air and leaf temperatures within and just above the ground cover layer (e.g., Figure 4). Although vertical growth through this low temperature zone may be critical for new seedling survival and sapling growth, surrounding structures can generate higher leaf temperatures during the day by reducing air flow; such structures also provide shade protection from excessive sunlight (Smith and Carter 1988, Smith and Brewer 1994). Ball et al. (1997) reported decreases in photosynthesis of *Eucalyptus pauciflora* Sieber ex A. Spreng. seedlings in response to low nighttime air temperatures just above a grass layer, and low nighttime needle temperatures also occurred in *Picea engelmannii* seedlings growing within grass cover of an alpine meadow in Wyoming (Germino and Smith 2002). Thus, sky

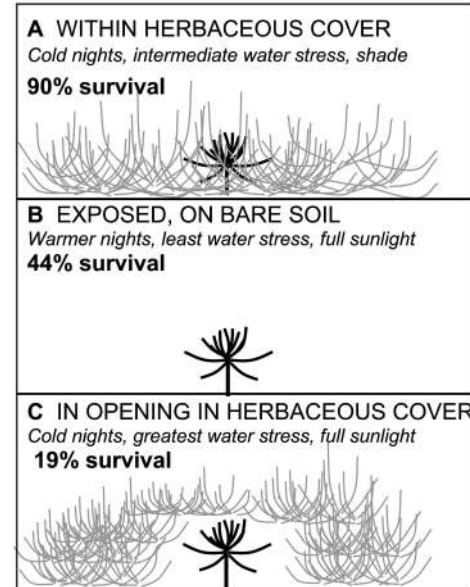


Figure 4. Microsite alteration experiment showing effects of facilitation versus competition on survival of new (first-year) seedlings of *Picea engelmannii* (Engelmann spruce) in an alpine treeline ecotone, southeastern Wyoming. Greatest survival (90%) occurred for seedlings growing in vegetative ground cover that resulted in low sky exposure and low incident sunlight the following morning, intermediate water stress, and relatively cold nights. Removing all vegetation well away from a seedling reduced competition for soil water (higher xylem water potentials), but increased sky exposure, resulting in significantly lower survival (44%). The highest mortality occurred when only proximal vegetation was removed to increase sky exposure while maintaining boundary layer effects, lower minimum needle temperatures and competition for water (as validated by higher water potential values). Higher photosynthetic carbon gain as a result of reduced low-temperature photoinhibition of photosynthesis was also associated with increased survival. Thus, facilitated reduction in sky exposure (day and night) appeared to have a greater influence on photosynthesis and survival than low temperatures or competition for water with neighbors, although all three factors had significant impacts (adapted from Germino and Smith 2002).

exposure can lower temperatures at night and increase temperatures during the day, depending on the balance between sun and nighttime sky as well as wind exposure (Figure 2).

Decreased sky exposure as a result of surrounding structures increases nighttime needle temperatures and also reduces insolation during early morning hours. These combined stresses can lead to substantial reductions in photosynthetic carbon gain as a result of low-temperature photoinhibition (Germino and Smith 1999, 2000a, 2001, Egerton et al. 2000). Microsite facilitation resulted in the highest survival rate of new seedlings at a high-elevation timberline site in the central Rocky Mountains, and also demonstrated a greater facilitative advantage than competitive disadvantage (Germino and Smith 2001, Figure 4). A similar increase in seedling survival in the shelter of krummholz mats has been reported for treeline conifer seedlings of the Rocky Mountains (Hättenschwiler and Smith 1999, Germino and Smith 2001). In addition, the needle clustering observed in sky-exposed seedlings (Germino and Smith



1999, Figure 5) and shoots of saplings and mature trees (Smith and Carter 1988) has been shown to raise needle temperatures during the day, resulting in increased photosynthetic carbon gain per needle area and stem length. Thus, convective and radiant energy exchange during the night and day, especially sky exposure and cold-air settling in the ground cover boundary layer, needs to be evaluated for its effects on seedling and sapling photosynthesis, respiration and other growth processes. And interactions between aerodynamic and sky-exposure effects, along with common leaf wetting events such as dew formation and cloud immersion (leading to possible strong influences on gas exchange), need to be evaluated with respect to the benefits of ecological facilitation on photosynthetic carbon gain (Brewer and Smith 1997).

### Mechanism of stem escape from krummholz mats

The mechanisms by which seedlings and saplings can grow vertically into forest-like trees may be analogous functionally to the development of flagged trees from krummholz mats (Figure 1 top panel). The development of a large enough krummholz mat in the direction of the prevailing wind reduces boundary layer wind speeds and abrasion at the downwind side of the mat, enabling the escape of vertical leaders (initially without needles and with only a single apical bud) that result in the characteristic flagged stems observed on the downwind edge of larger krummholz mats (Figure 1 top panel). None of the vertical leaders that have grown through the abrasive boundary layer have needles at their base, although subsequent stems branching higher on the main flagged stem have increasing leaf numbers (Figure 1). The ex-

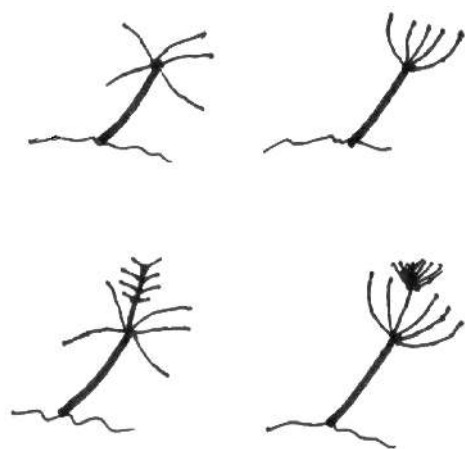


Figure 5. Architecture of first-year seedlings with cotyledons only (top), with low (left) and high (right) exposure to the sky (cold night sky and maximum solar irradiance), as well as older seedlings with first primary needles present following initial bud burst (bottom). A more upright needle orientation and clustering of cotyledons and primary needles implicates structural (self-) facilitation that minimizes sky and sun exposure (cold night sky and daytime sunlight), leading to higher cotyledon/needle temperatures at night. Thus, low temperature effects on photosynthetic carbon gain the following day, as well as on growth processes, are reduced.

istence of secondary branches on the leeward side of the main stem, with needles only on their leeward sides, are examples of increased survival within an aerodynamic boundary layer generated by the whole-plant structure. Many conifer tree species are apparently incapable of the architectural plasticity necessary for survival at treeline, e.g., many pine species (Hadley and Smith 1987).

The wedge-like shaping and lengthening of a single krummholz mat away from the direction of the prevailing winter wind generates greater frictional drag and a lowering of wind speeds on the leeward end of the mat (Figure 3B). The increasing abundance of tree forms per unit ground area provides more shelter from wind and sky (Figures 3A and 6). For newly emerged seedlings in the treeline ecotone, this protection appears to come initially from microsite (animate and inanimate) and structural facilitation (Figure 5), followed by the greater intraspecific and interspecific facilitation that results in snow capture and protective winter burial (Figure 1, Hättenschwiler and Smith 1999, Moir et al. 1999). The same facilitation may also reduce exposure to sun and cold night skies, leading to greater photosynthetic carbon gain and survival (Germino and Smith 2001, 2002). Just as the larger size of a krummholz mat can result in the vertical growth of stems from its leeward edge (Figure 1 middle panel), a greater abundance of seedlings and, ultimately, mats and tree islands will also reduce wind speed and sky exposure (day and night) to the extent necessary for the growth of a forest-like tree within a new subalpine forest at higher altitude (Figures 2 and 6).

### Horizontal fusion of tree forms

It is possible that the horizontal spreading (e.g., layering) of existing stunted, flagged or mat-like trees and tree clusters (Figure 3) could contribute to the formation of new subalpine forest at higher altitude. If so, fewer seedlings would have to establish themselves on a unit ground area basis to move the timberline upward. However, there is evidence that the tree growth forms occurring in treeline ecotones do not merge horizontally, even over distances of only a few meters (e.g., Schönenberger 2001). This scenario also seems unlikely because seedling establishment appears to respond quickly and positively to the presence of established tree forms. For example, a strong facilitation by mature trees in the treeline ecotone was associated with a much greater seedling abundance found beneath, and close to, existing tree structures (Holtmeier and Broll 1992, Callaway 1998, Hättenschwiler and Smith 1999, Germino and Smith 2002).

Apical leaders located on the sides of krummholz mats experience the same abrasive impacts of blowing snow, and are eliminated in the same fashion as the vertical leaders on the tops of mats (Hadley and Smith 1989). These effects act in concert to generate the wind-tapered, conical shapes common to most krummholz mats with or without flagged stems on their leeward ends (Figures 1, 3 and 6). Also, these larger mats tend to accumulate deeper snowdrifts on their leeward sides that may persist well into summer. The needles on the branches of

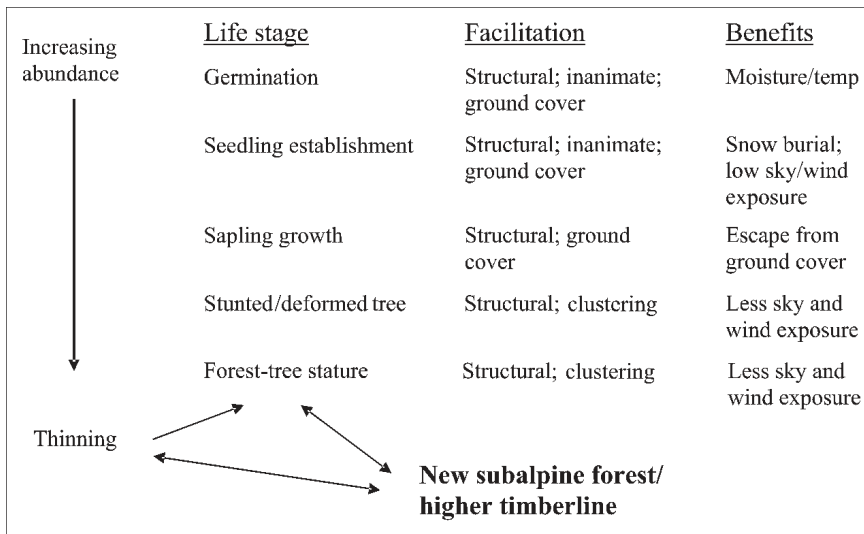


Figure 6. Idealized stages of ecological facilitation involved in the formation of new subalpine forest at higher altitude. The type of facilitation and corresponding benefits are listed for each life stage. Arrows indicate the interaction necessary for the development of a forest tree within new subalpine forest at higher elevation. See text and Figure 2 for further details of the possible physiological benefits of facilitation to carbon gain and growth processes leading to the upward migration of a timberline.

the leeward sides often die from snow mold infection (Wardle 1968, Marr 1977), inadequate seasonal carbon gain because of prolonged burial, or both. Thus, too little, as well as too much, wind exposure and snow accumulation appears to limit the size and horizontal fusion of individual krummholz mats (Figure 1 top panel, Hättenschwiler and Smith 1999). If horizontal fusion of neighboring tree forms is uncharacteristic of treeline ecotones, then the abundance of seedlings and saplings may be critical to the facilitated formation of new subalpine forest and a higher timberline.

### Ribbon forest at timberline

In wind-exposed timberlines that are more or less perpendicular to the direction of prevailing winds, a ribbon-like forest develops at the leading edge of the intact forest timberline (Billings and Mark 1957, Arno and Hammerly 1990, Figure 1). This appearance is generated by an extraordinarily heavy snow deposition just behind the leading row of trees that generates a treeless snowglade with severely distorted tree forms on its borders. This is sometimes referred to as the “snow fence” effect when heavy and prolonged snow accumulation prevents seedling establishment. If wind speeds are great enough, ribbons of trees may occur for several layers back into the forest. These ribbons migrate upward as the lower ecotone becomes filled with additional tree forms, reducing sky and wind exposure. A greater density of ecotonal trees (in all forms) will act as an advancing snow fence and cause the heavy snow deposition lines (snow glade) to shift upward in elevation. Thus, the increased seedling/sapling abundance leads to an upward shift of a ribbon forest.

### Significance of facilitation

Microsite facilitation generated structurally, intraspecifically or interspecifically may be critical for initial seed germination and successful seedling establishment in treeline ecotones (e.g., Ball 1994, Ball et al. 1997, Germino and Smith 1999,

2000b, 2002, Figures 4 and 5). Subsequently, continued facilitation as a result of the increased abundance and cover of new saplings of one or more tree species may also influence the process by which timberlines and treelines advance upward (Figure 6). Thus, Hypotheses 2–5 for timberline causation (Table 1) may be most relevant in terms of their influence on Hypothesis 1. The germination, survival and successful establishment of ecotonal seedlings and their subsequent growth into saplings facilitates recruitment and growth rates approaching those found in an intact subalpine forest. Figures 2 and 5 summarize the seasonal facilitation of different growth stages necessary for the ultimate formation of new subalpine forest at higher altitude, plus the abiotic environmental factors known to limit photosynthetic carbon gain and seedling survival. For the same reason that a flagged stem escapes initially as a vertical leader on the downwind edge of a krummholz mat, trees with more forest-like stature begin to form beyond the timberline as a result of microsite facilitation (reduced wind and sky exposure) provided by a variety of tree forms (Figure 1 middle panel). Thus, increased seedling abundance is a prerequisite for generating the facilitation necessary for the migration of a timberline upward. This trend of increased abundance providing greater facilitation may be reversed when low solar irradiance limits the benefit of clustering. Because of shade limitations on photosynthesis and growth, a final thinning stage is often required before the development of trees with forest-like stature occurs in most subalpine forests (e.g., Alexander 1967, Knight 1994, Figure 5).

This scenario of facilitation implies that the final stage of seedling and sapling growth to undistorted, forest-tree stature requires a degree of facilitation approaching that found in intact forest. Moreover, this general sequence of facilitation processes may underlie the mechanisms of distributional shifts across other boundary ecosystems for a variety of species. The importance of facilitation in alpine communities has been reported previously for the northern Rocky Mountains (Callaway 1998) and the southwestern Alps (Choler et al. 2001), in addition to all other plant biomes (e.g., Callaway



1995). More work is needed to clarify the mechanisms of facilitation involved in successional systems responding to natural or anthropogenic perturbation, and specific impacts on community structure and composition.

### Treeline ecotones with small, undistorted tree forms

It might be argued that conditions at timberlines with abrasive, blowing snow crystals and severe growth form distortion (Figure 1) are extreme compared with those at other timberlines worldwide. However, the numerous photographs and drawings of alpine ecotones in Arno and Hammerly (1984) show krummholz, flagged and stunted tree forms throughout North and Central America, and elsewhere in the world (including both temperate and tropical timberlines in both hemispheres). The distinctive clustering of trees to form islands and ribbons is also evident in these photographs. Additional observations and photographs of treelines in Europe, Japan, China, Hawaii, Peru, New Zealand, Australia and Georgia (W. K. Smith, unpublished data) show a common pattern in structural characteristics ranging from stunted trees with nearly forest-tree stature to dramatically deformed trees (e.g., krummholz forms). When timberlines do not have severely distorted growth forms, but simply dwarf trees, it seems reasonable that other abiotic factors such as increased sky and wind exposure (e.g., low minimum temperatures, high sunlight) could be limiting growth. Even tropical treelines can experience near- or below-freezing nights throughout the entire year. Even if relatively mild conditions prevail compared with the temperate zone, carbon acquisition and processing for growth could be enhanced by generation of a more favorable microclimate. Microsite facilitation at high elevation or latitude can also result in conditions that are identical to those at a site at a much lower elevation or latitude without facilitation. In short, the same microsite conditions leading to severe wind abrasion of leaf cuticles at a higher altitude might result only in a colder seedling that is susceptible to low-temperature photoinhibition (greater sky exposure) at lower elevation.

### Atmospheric dryness and the alpine treeline

Long-term tree ring studies indicate that periods with higher temperatures correspond with periods of increased seedling establishment at several treeline locations, but only in combination with increased water availability (e.g., Hessel and Baker 1997). Cui and Smith (1991) and Germino and Smith (1999, 2001, 2002) have also associated carbon gain limitations as a result of photoinhibition with decreased root growth, mycorrhizal infection and apparent mortality by desiccation in both understory conifer seedlings and treeline seedlings. Neuner et al. (1999) concluded that low-temperature photoinhibition of photosynthesis in exposed leaves (incomplete snow cover) was closely linked to winter desiccation in an evergreen species at timberline in Austria. We note that ambient air pressure—a physical property that has a strong influence on plant water relations at high elevation—may be one abiotic factor

that cannot be influenced by microsite facilitation. The diffusion coefficient for water vapor increases substantially with decreasing pressure at higher altitudes, leading to transpiration rates typical of much warmer climates (Smith and Geller 1981, Smith and Knapp 1985). In contrast to the compensating effect of more rapid mass diffusion rates at high elevation, which offset low ambient CO<sub>2</sub> partial pressures, water vapor loss can be expected to be substantially greater at high elevation for the same CO<sub>2</sub> uptake at lower elevation. Greater solar irradiance and lower air temperatures result in leaf temperatures that are above air temperature with a particularly strong water vapor gradient, although few data are available for comparisons of leaf-to-air vapor pressure differences at higher elevations (Smith and Knapp 1985). This large leaf-to-air water vapor gradient, combined with the greater diffusion coefficient at lower ambient pressure, results in greater transpiration at a given value of CO<sub>2</sub> uptake. Even tropical alpine areas have been shown to be exceptionally xeric for this reason. Leuschner (2000) concluded that tropical alpine treelines may be dryer than those of the temperate zone, with transpiration rates estimated to be 50–90% higher than for the same altitude in temperate latitudes. Although reports of stomatal changes in response to altitude are rare (Körner et al. 1989), the frequency of stomata per unit needle mass decreased with elevation in pine, spruce and fir species (Hultine and Marshall 2000). Problems associated with plant hydraulics and effects of freeze-thaw cycles on xylem cavitation may also be exacerbated at high elevation because of the frequency of near-freezing temperatures, in combination with high evaporative demand (Rada et al. 1996), which may be strongly influenced by microclimate and plant form facilitation. Drought stress has been associated with the elevation of the treeline found on Mt. Haleakala in Hawaii (Leuschner 1991), and historically warmer conditions may have resulted in a decline in treeline elevation when accompanied by drought (Lloyd and Graumlich 1997). Little is known about the potential effects of clustering on ambient vapor pressure. Kikvidze (1996) reported that neighboring vegetation increased photosynthesis substantially in *Trifolium ambiguum* Bieb. plants in a subalpine meadow in full sunlight, but caused declines under cloud cover. It is possible that increased water vapor pressure within the ground cover layer could lead to greater stomatal opening and photosynthesis. Thus, effects of ecological facilitation on water relations of establishing seedlings, as well as on sapling growth, need to be evaluated as factors interacting with photosynthetic carbon gain and respiratory processes in alpine treeline species. For example, little is known about the potential effects of ground cover on the ambient humidity experienced by young conifer seedlings, even though desiccation has been associated with the high mortality at treeline (Germino and Smith 2002) and in subalpine forest (Knapp and Smith 1981, Cui and Smith 1991).

### Conclusions

We hypothesized that the upward migration of a timberline or

treeline was dependent on ecological facilitation within the transitional ecotone, beginning with seed germination and continuing until the growth of mature forest-like trees (Figure 6). New seedlings in the treeline ecotone of the Rocky Mountains that were unprotected by microsite facilitation succumbed to an apparent desiccation death (usually in their first or second year of growth). Seedling death was associated with limitations to photosynthetic carbon uptake, poor root growth, lack of mycorrhizal infection and low water status. These limitations to carbon gain may involve both daytime and nighttime factors. Because of apical leader mortality in winter, but high lateral shoot survival, high-density mats (LAI > 20) accumulate snow and provide an insulated environment in which lateral branches can survive winter (Figure 1). Apical leaders that develop in summer but are not buried beneath snow the following winter are injured by the wind and ice crystal layer next to the snow surface and die from cuticle abrasion and desiccation. Reductions in wind speed, however, allow vertical leaders on the downwind side of a krummholz mat to grow through the boundary layer next to the snow surface and extend vertically (Figure 3B). For each vertical leader that escapes, mutual sheltering (structural facilitation) enables the survival of adjacent leaders. These steps of stem escape from a krummholz mat, the development of larger mats with more flagged trees on their downwind edges and finally, the appearance of larger tree islands at the subalpine forest edge all point to the functional importance of facilitation in the environment of alpine treelines (Figures 1, 3 and 6). Moreover, facilitation appears to depend on continuing increases in seedling/sapling abundance. A similar facilitation scenario has been taken as the basis for a European management plan to restore high-elevation forests ("Cluster Afforestation" or "Rottenpflanzung"; Schönemberger 2001).

More evidence is needed to validate the hypothesis that growth limitation (carbon sink) is a greater determinant of timberline altitude than photosynthetic carbon gain (source), especially for establishing seedlings. Circumstantial evidence that assimilated carbon remains relatively constant for mature trees, even under high demand growth conditions and during periods of low assimilation, may only reflect the adaptive importance of maintaining stored carbon reserves in response to extreme and highly variable environments. It is tempting to conclude that recent anthropogenic increases in atmospheric CO<sub>2</sub> could lead to asynchrony between carbon assimilation and respiratory processing for growth, but definitive evidence is unavailable. However, given that historical CO<sub>2</sub> concentrations have fluctuated between much lower and higher values (> 2000 ppm) as far back as the Cretaceous, this hypothesis seems tenuous (e.g., Nordt et al. 2002, Osbourne and Beerling 2002). More research is needed to evaluate directly a scenario in which respiratory-driven growth processes can become asynchronous with carbon acquisition, beyond the advantage of carbon pooling for exigencies. Such information could be valuable for predicting future altitudinal shifts in subalpine forests under different scenarios of global climate change.

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