

Altitudinal and Polar Treelines in the Northern Hemisphere – Causes and Response to Climate Change

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Abstract: This paper provides an overview on the main treeline-controlling factors and on the regional variety as well as on heterogeneity and response to changing environmental conditions of both altitudinal and northern treelines. From a global viewpoint, treeline position can be attributed to heat deficiency. At smaller scales however, treeline position, spatial pattern and dynamics depend on multiple and often elusive interactions due to many natural factors and human impact. After the end of the Little Ice Age climate warming initiated tree establishment within the treeline ecotone and beyond the upper and northern tree limit. Tree establishment peaked from the 1920s to the 1940s and resumed again in the 1970s. Regional and local variations occur. In most areas, tree recruitment has been most successful in the treeline ecotone while new trees are still sporadic in the adjacent alpine or northern tundra. Lack of local seed sources has often delayed tree advance to higher elevation. New trees established above the present seed trees and ancient solitary trees far above the present forest limit which survived cool periods without being able to reproduce from seeds may now become effective seed sources and encourage further upward shift of the treeline ecotone. At exposed sites warming cannot compensate for growth disturbances caused mainly by winter injury and biotic factors. Extreme climatic events may cause lasting setbacks at any time. Microsite facilitation is of particular importance for the survival of seedlings and saplings above the closed mountain forest stands. The relative importance of microsite facilitation will increase in parallel with the upslope migration of the tree limit into a much windier environment. Treeline migration to higher elevations and a more northern position is bringing about fundamental changes in high mountain environments and at the tundra-taiga interface which will also influence the local economy.

Zusammenfassung: Dieser Artikel gibt einen Überblick über die Ursachen sowie die regionale Verschiedenartigkeit der oberen und nördlichen Baumgrenzen und vermittelt einen Einblick in deren Heterogenität und Reaktion auf die sich verändernden Umweltbedingungen. In globaler Sicht ist die Lage der oberen und polaren Waldgrenze primär durch den Wärmemangel bedingt. Kleineräumig betrachtet hängen ihre Lage und räumlichen Strukturen von einer Vielzahl natürlicher und anthropogener Faktoren ab, die sich wechselseitig in oft schwer durchschaubarer Weise beeinflussen. Die Erwärmung seit der „Kleinen Eiszeit“ hat zu einer Ausbreitung des Baumwuchses im Baumgrenzökoton und über die obere und polare Baumgrenze hinaus geführt, mit einem Maximum während der 1920er bis 1940er Jahre. Seit den siebziger Jahren des vorigen Jahrhunderts hat sie wieder zugenommen, mit regionalen und lokalen Unterschieden. In den meisten Gebieten hat sich der Baumwuchs am erfolgreichsten innerhalb der Baumgrenzökotone ausgebreitet, während Jungwuchs in der angrenzenden alpinen Stufe und in der Tundra immer noch vergleichsweise selten ist. Häufig hat das Fehlen lokaler Samenquellen das Vordringen des Baumwuchses in größere Höhe verzögert. Jetzt aber können die bereits oberhalb der gegenwärtigen Samenbäume etablierten jungen Bäume wie auch vereinzelte uralte Exemplare weit über der gegenwärtigen Waldgrenze, die kühlere Perioden überlebt haben, ohne sich durch Samen vermehren zu können, zu wichtigen Samenlieferanten werden und das Vordringen des Baumwuchses beschleunigen. An exponierten Standorten kann die Erwärmung die vor allem durch winterliche Schäden und biotische Faktoren verursachten Wachstumsstörungen nicht kompensieren. Rückschläge infolge extremer Ereignisse sind jederzeit möglich. Oberhalb der geschlossenen Waldbestände kommt der Begünstigung des Jungwuchses durch Schutz bietende kleinstandörtliche Bedingungen eine besondere Bedeutung zu. Ihr Einfluss wird mit

dem Vorrücken der Baumgrenze in größere, wesentlich windigere Höhen relativ zunehmen. Die Verlagerung der Baumgrenze in größere Höhen und weiter nach Norden wird zu grundlegenden Veränderungen der Landschaft in den Hochgebirgen und am Rande von Subarktis/Arktis führen, die auch wirtschaftliche Folgen haben werden.

INTRODUCTION

Global warming since the end of the “Little Ice Age” (about 1900) is bringing about socio-economic changes, shrinking glaciers, melting permafrost, rising sea level, changes in the precipitation regimes, lengthening of the snow-free season, expansion and extinction of species and shift of vegetation limits, among them the altitudinal and polar treelines.

In the present paper the term treeline means the transition zone (synonyms: treeline ecotone, forest-tundra ecotone, forest-alpine tundra ecotone) extending from the upper limit of closed subalpine or northern forests (= forest limit) to the uppermost or northernmost scattered and usually stunted individuals of the forest-forming tree species (= tree limit, tree species limit) (see HOLTMEIER 2009 for terminology).

Treelines are among the most conspicuous vegetation limits. Their position and physiognomy vary however regionally and locally. No wonder that the treelines have attracted scientists from many disciplines. They have produced an immense wealth of literature (see ample references in HOLTMEIER 2009). This review is based on the authors' field research (high mountains of Western North America, Alps, northern Europe) and on treeline-relevant literature. The paper addresses to a broader readership rather than to treeline experts and gives an overview on the heterogeneity and regional variety as well as on the response of both altitudinal and northern treelines to the changing environmental conditions. It is the great physiognomic, biological and ecological diversity of the altitudinal and northern treelines which should be considered as the essential feature in the global treeline pattern.

MAIN CHARACTERISTICS OF TREELINE

The northern treeline often occurs as an altitudinal boundary. Due to its high latitudinal position it is located at comparatively low elevations. While in subarctic lowlands the forest-tundra ecotone may extend over some tens or even hundreds of kilometres, the ecotone is relatively narrow on subarctic mountains. In the temperate high mountains, the maximum width of the treeline ecotone usually does not exceed a few hundred meters. Normally it is much narrower.

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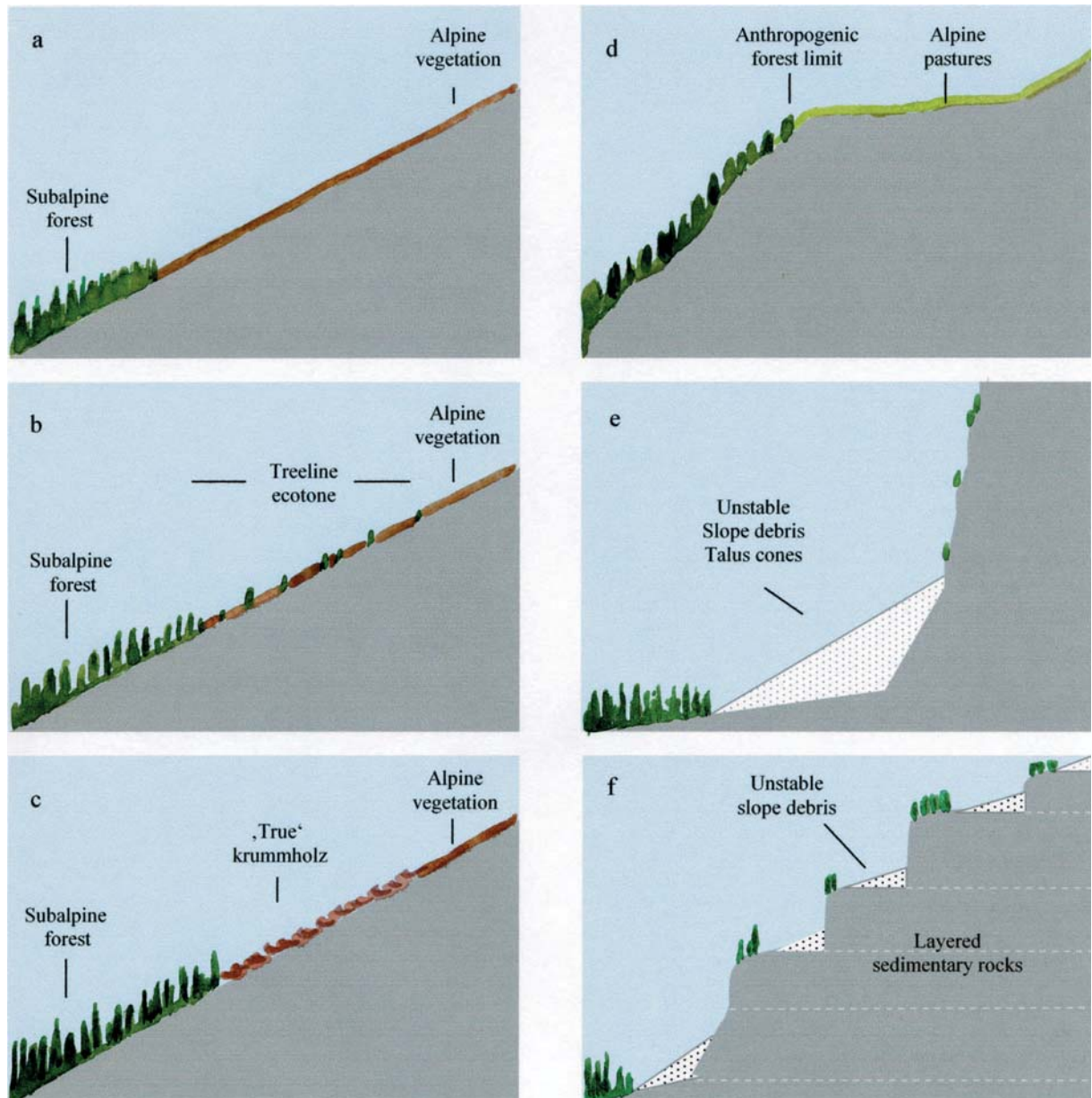


Fig. 1: Types of climatic and some other treelines. a = abrupt limit of closed forest. b = transition zone (treeline ecotone). c = "true" krummholz belt above the upright growing forest. d = anthropogenic tree line located at the upper rim of the steep trough wall. e = treeline caused by unstable slope debris. f = treeline on a steep slope characterized by structural benches alternating with unstable slope debris.

Abb. 1: Klimatische und einige andere Baumgrenztypen. a = Scharfe Waldgrenze. b = Übergangssaum (Baumgrenzökoton). c = „echter“ Krummholzgürtel oberhalb des hochstämmigen Waldes. d = am oberen Rand einer steilen Trogwand gelegene anthropogene Baumgrenze. e = durch instabilen Hangschutt verursachte orographische Waldgrenze. f = Baumgrenze auf einem durch ausstreichende Schichtköpfe im Wechsel mit instabilem Hangschutt geprägten Steilhang.

Climatic treelines (Fig. 1a-c) may be abrupt or occur as a more or less wide transition zone between the closed forest and the tree-limit. In some mountain areas the high-stemmed forest gradually merges into a belt of "true" krummholz (HOLTMEIER 1981) such as dwarf mountain pine (*Pinus mugo*) or Siberian dwarf pine (*Pinus pumila*) bordering the mountain tundra. Anthropogenic treelines, particularly those, which are located at the upper rim of steep trough walls, are also usually abrupt (Fig. 1d). Unstable slope debris, talus cones and steep rock walls may cause an abrupt forest limit at relatively low elevation, while solitary trees and tree groves may occur far above at sites safe from disturbances (Fig. 1e,f).

In the Northern Hemisphere, the treeline is formed in most parts by conifers such as spruce, fir, pine, larch, and juniper. Regionally, deciduous species (e.g., birch, beech, aspen, rhododendron) also occur. Approaching the treeline, tree height usually decreases and more or less climatically stunted growth forms increase (Fig. 2).

The treeline ecotones are characterized by specific ecological and climatic conditions, which differ from those of the closed subalpine or northern forests and of the alpine and northern tundra. Thus, a climatically-caused shift of the treeline ecotone to higher elevations and a more northern position will bring about fundamental changes in high mountains as well as in



Fig. 2: Treeline ecotone (*Picea engelmannii*, *Abies lasiocarpa*) on the west slope of the Colorado Front Range at about 3600 m. In the upper part of the ecotone, tree height decreases rapidly. Photo F.K.H., 4 September 1977.

Abb. 2: Baumgrenzökoton (*Picea engelmannii*, *Abies lasiocarpa*) auf dem Westhang der Colorado Front Range in rund 3600 m Höhe. Im oberen Bereich des Ökotonns nimmt die Baumhöhe rasch ab. Foto F.K.H., 4. September 1977.

subarctic and arctic environments.

TREELINE-CONTROLLING FACTORS

To understand treeline dynamics a great number of factors influencing tree growth, regeneration, survival and site conditions have to be considered (Fig. 3). Moreover, we have to switch between different scales of consideration (global, zonal, regional, local, microscale to approach the complex phenomenon (HOLTMEIER & BROLL 2005, HOLTMEIER 2009, MALANSON et al. 2009). At regional and smaller scales, for example, historical disturbances by natural factors and human impact, usually interacting in a complex way, determine the position and spatial patterns of treelines while the current climate often has only a modulating effect (cf. Fig. 3 and Fig. 14). In many areas, the present position of the treeline has to

be ascribed even for the most part to landscape-, climate- and site-history rather than to the present climate (HOLTMEIER 1965, 1974, 2009, HOLTMEIER & BROLL 2005, 2007). Thus, projecting empirically found relationships between the position of the current treeline and certain isotherms into the future will possibly underestimate any lasting effects of treeline geographical history. Not least, temporal scales of consideration must not be disregarded.

Climate

From a global viewpoint, climatic treeline position can be considered to be caused mainly by heat deficiency; i.e. by short and often cool growing seasons. Heat deficiency increases with elevation and latitude. Treeline position has often been ascribed to the coincidence of specific isotherms

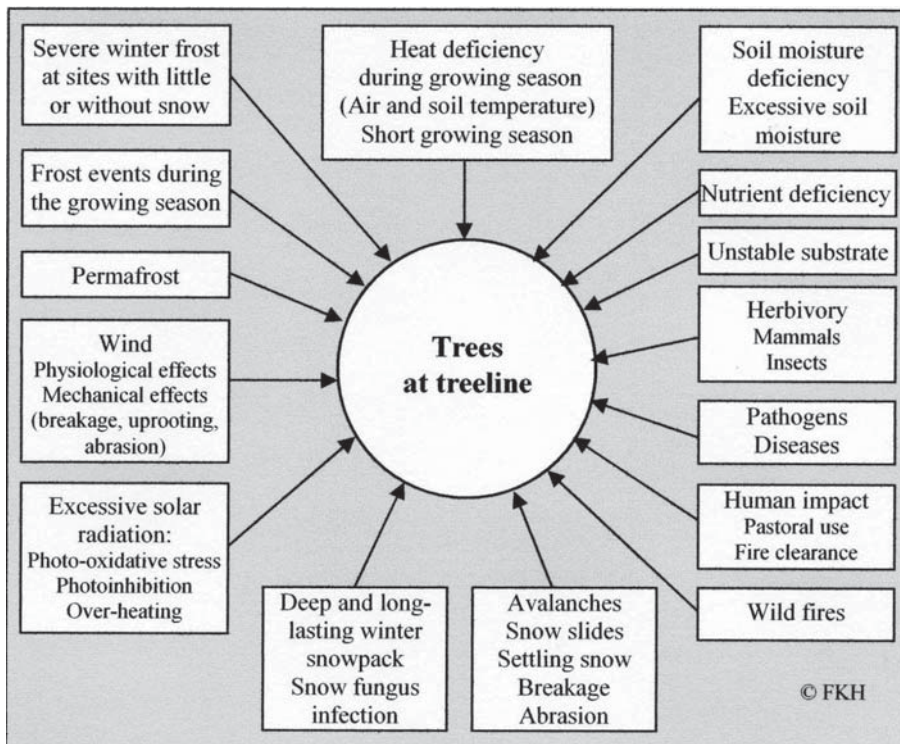


Fig. 3: Factors affecting trees at the altitudinal and polar treelines.

Abb. 3: Den Baumwuchs an der oberen und polaren Baumgrenze beeinträchtigende Faktoren.



considered to be controlling tree growth, such as the mean air temperature of the warmest month or the three or four warmest months, for example. Also, the number of 5 °C days (mean daily air temperature) and thermal sums during the growing season are used to explain treeline position. More recently a mean soil temperature of 5 °C to 7.5 °C of the growing season has been put forward to be controlling worldwide treeline position (KÖRNER 1998a, 1999). In contrast to the coincidences of treeline position and other isotherms, this temperature comes closer to the critical thermal threshold of +5 °C below which biochemical processes are generally impeded (e.g., RETZER 1974).

Apart from low soil temperature there are many other climatic factors affecting tree growth at high elevations and in the north (cf. Fig. 3). For example, frost, mainly late and early frosts, may injure plant tissue that are insufficiently developed or de-hardened. In particular seedlings are sensitive in this respect. Strong winds may cause mechanical damage (abrasion, breakage, uprooting) and physiological injury (e.g., winter desiccation) before low soil temperatures limit tree growth (HOLTMEIER 2009). In addition, photo-oxidative stress and photo inhibition due to excessive radiation loads at high altitudes may also be injurious (e.g., BALL et al. 1991, GERMINO & SMITH 1999, SMITH et al. 2003, JOHNSON et al. 2004, TAUSZ 2007, BADER et al. 2008). Such injuries may be critical to seedling survival despite mean daily minimum temperature of the growing season being high enough not to impair growth processes.

It has long been discussed whether photosynthetic carbon deficiency limits tree growth at high elevations. Whereas negative carbon balances due to respiratory losses were occasionally observed (e.g., SCHULZE et al. 1967, UNGERSON & SCHERDIN 1968, TRANQUILLINI 1979, GERMINO & SMITH 1999) no long-term carbon deficiency (carbon source limitation) was however measured that would determine treeline position. Instead of limited carbon gain, limitation of metabolic carbon investment (carbon sink hypothesis) has been suggested to be the most important effect of low temperatures (KÖRNER 1998a, 2007, HOCH et al. 2002, HOCH & KÖRNER 2003, 2005). As a result, carbon reserves in treeline trees will usually not be depleted. Dry matter production may however be drastically reduced from time to time by high needle losses (GERMINO & SMITH 1999, SVEINBJÖRNSSON et al. 1996, JOHNSON et al. 2004). In any case, in all of our treeline study areas a growth increment is apparent even in the most severely stunted tree outposts, even although it may be very small or the trees may occasionally show missing growth rings reflecting unfavourable growing conditions.

Topography

Topography (landscape surface) almost is a constant factor among the many treeline-influencing agents. Most other factors, such as solar radiation, windflow near the surface, temperatures, soil moisture, length and depth of the winter snow cover and its resultant effects, distribution of soil types, and site conditions in general are controlled and modified by the given geomorphic structure (AULITZKY 1963, HOLTMEIER 1974, HOLTMEIER 2005, BROLL et al. 2007, BUTLER et al. 2007). The influences of topography on site conditions, as on

the distribution of soil moisture for example, may be different under different climates. Moisture deficiency on convex topography for example may be mitigated when the climate is becoming more humid whereas it would exacerbate in a drier climate (HOLTMEIER & BROLL 2005). The effects of similar microtopography on solar radiation, wind and snow cover also vary according to the particular situation (HOLTMEIER 2005, 2009).

Steep rock walls, mass wasting, slope debris, talus cones and avalanche tracks usually prevent forest from reaching its possible climatic altitudinal limit (cf. Fig 1e,f). On steep slopes, orographically-caused treelines appear to be more common than true climatic treelines (HOLTMEIER 2009). Topography also sets limits to human land use (cf. Fig 1d). After all, topography controls the spatial pattern of treeline and modulates the effects of the regional climate on treeline dynamics at the landscape and local scales.

Human impact

In most of the mountains of Europe and Asia, which were already settled in prehistoric time, manifold forest use and fire have lowered the altitudinal treeline during history almost everywhere where topography was not steep enough to prevent access. The extent of treeline depression however varied regionally (HOLTMEIER 2009 *cum lit.*). In trough-shaped valleys (Alps, Norwegian Fiordland), for example, the original forest was removed from the trough shoulders to create alpine pastures, and the treeline became located at the upper rim of the steep and almost inaccessible trough walls (cf. Fig. 1d). Moderate slopes became often completely deforested, in particular on southern aspects whereas forests on steep valley sides were usually less affected. In the Alps, for example, a treeline depression of 150-300 m below its maximum Holocene position can be accepted as an average value (e.g., HOLTMEIER 1974, BURGA & PERRET 1998).

Although usually located in remote areas, the northern treeline has also been, and still is, influenced by human activity, mainly by reindeer grazing exceeding the natural carrying capacity of the forest-tundra ecotone and by cutting fire wood (HOLTMEIER, 2009). Overgrazing by semi-domestic reindeer is mainly affecting establishment of new trees in the treeline ecotone (e.g., HOLTMEIER 2002, LEMPA et al. 2005, NEUVONEN & WIELGOLASKI 2005, ANSCHLAG et al. 2008).

Wild-living animals

In the treeline ecotone on high mountains farther south, excessively high populations of wild-living ungulates such as red deer (*Cervus elaphus*) in the European Alps or American elk (*Cervus canadensis*) and mule deer (*Odocoileus virginianus*) in the Rocky Mountains, may locally impede or even prevent tree recruitment within the treeline ecotone and in the alpine tundra by browsing, bark-stripping and trampling. "Oversized" ungulate populations are mainly the result of landscape and land use change and inappropriate game and habitat management. In general, wild ungulates do harm to the treeline trees rather than having any positive effects (HOLTMEIER 2002, 2009).

Burrowing animals (e.g., ground squirrels, pocket gophers, marmots) expose the mineral soil and thus create open patches that may facilitate the establishment of seedlings, sufficient soil moisture and protection from wind provided. On the other hand, they may cause serious damage to seedlings and saplings by gnawing and girdling the stems and twigs buried under the winter snowpack.

Birds influence the treeline ecotone mainly by dispersal of tree seeds. Nutcrackers (*Nucifraga caryocatactes* and subspecies in Eurasia, *Nucifraga columbiana* in North America) are the most important factor in this respect. Nutcrackers disperse the heavy wingless seeds of several stone pine species within the existing treeline ecotone and beyond tree limit where they hoard the seeds in subsurface caches on which they rely for food in the winter and spring (HOLTMEIER 1966, 2002, 2009, TOMBACK 1977, MATTES 1978). Seeds not used by the nutcracker may give origin to stone pine seedlings (cf. Fig. 10). Thus, these birds are a driving factor in treeline dynamics in their areas of distribution (see map in HOLTMEIER 2009).

TREELINE RESPONSE TO THE CHANGING CLIMATE

Treelines have been fluctuating throughout the Holocene due to changing temperatures and reached their maximum altitudinal position during the postglacial thermal optimum (4000-5000 BP) and then gradually declined due to a general cooling (e.g., BURGA & PERRET 1998, TINNER & KALTENRIEDER 2005, JENSEN & VORREN 2008). In most high mountains of Europe and Asia, which were already settled in prehistoric time human impact has enforced treeline decline (cf. HOLTMEIER 2009 *cum lit.*). Reports on treeline migration are often hard to compare because they often result from accelerated growth and release of vertical stems of formerly suppressed growth forms (e.g., mat-growth, table-growth, wedge-like growth, LESCOP-SINCLAIR & PAYETTE 1995, KULLMAN 2000, cf. Figs. 6, 8 and 11) rather than from the establishment of new trees within and beyond the treeline ecotone.

Regional variation

Since the end of the "Little Ice Age" treelines have been advancing in pulses. Infilling of treeless gaps within the treeline ecotone by new trees and tree establishment beyond the existing tree limit peaked during the favourable 1920s to the 1940s and, after a break, resumed since the 1970s. However, warming and treeline advance were not always synchronous and occurred at different regional and local intensities.

In the Kenai Mountains (south-central Alaska) for example, the treeline ecotone (*Picea glauca*) moved upwards on cool and presumably moderately moist north-facing slopes while on warm aspects shrub and tree population increased but the treeline ecotone did not advance (DIAL et al. 2007). On the Seeward Peninsula and in the Tanana-Yukon uplands (near Fairbanks, Alaska) as well as in many places on the Alaska Range, white spruce advanced far beyond the outmost forest stands (HOPKINS 1972, VIREECK 1979) whereas in the eastern parts of the mountain range no comparable changes occurred (DENTON & KARLEN 1977). In south-west Yukon, warming during the 1920s caused increased white spruce population

and a significant treeline advance on southern aspects during the early to mid 20th century while no upslope spruce migration occurred on north-facing slopes (DANBY & HIK 2007). In the Polar Urals, the treeline moved upwards by 20-50 m at an average during the previous century. On gentle slopes, the treeline advanced by 100-400 m into the mountain tundra (DEVI et al. 2008). In Mid-Siberia, the northern treeline has shifted by 90-300 m between the 1970s and 2000 (KHARUK et al. 2006). For the northern Alaskan treeline a northward shift by 2500 m has been estimated (LYOYD 2005). On the extremely snow-rich west slope of Mount Rainier (Washington), tree establishment has been almost continuous since about the 1930s, whereas cool, wet summers promoted supported tree recruitment on the east side where winter snowpack is lower (ROCHEFORT & PETERSON 1996).

In some areas, the tree population has increased mainly within the treeline ecotone while no new trees have become established beyond the current tree limit as has been reported from the northern treeline near Churchill (Hudson Bay) (SCOTT et al. 1987a, 1987b), for example, from the treeline east of Hudson Bay (GAMACHE & PAYETTE 2005) and in the Northwest Territories (SZEICZ & MACDONALD 1995). In many places, however, seedlings and saplings now occur far beyond the tree limit as for example in some areas of the Swedish Scandes (KULLMAN & ÖBERG 2009) and of the Rocky Mountains (BUTLER et al. 2004, HOLTMEIER 2009). In Norway, treeline has been stable or is advancing in the southernmost and probably in the middle regions while it is retreating in the north (DALEN & HOFGAARD 2005).

Moreover, the response of the treeline-forming tree species to the warming climate has been different according to their specific ecological properties and requirements and to the site conditions. At the upper treeline in the northern Urals, for example, birch (*Betula tortuosa*) has expanded most intensively while the proportions of Siberian spruce (*Picea obovata*) and in particular of Siberian larch (*Larix sibirica*) have decreased. Successful expansion of birch is explained by climate warming and in particular by increased summer and winter precipitation. Local differences are however apparent. Larch is more successful than birch on dry windy sites, which are almost devoid of snow in winter and where it does not have to compete with other tree species (KAPRALOV et al. 2006). In the southern Urals, Siberian spruce is the pioneer tree invading the mountain tundra first, followed by birch (*Betula tortuosa*) and mountain ash (*Sorbus aucuparia*) which profit from the shelter given by spruce. The latter will out-compete the deciduous tree species in the course of natural succession invading the mountain tundra first (MOISEEV & SHIYATOV 2003).

On Beartooth Plateau (Montana/Wyoming), great numbers of whitebark pine seedlings (*Pinus albicaulis*) have originated from seed caches of the Clark's nutcracker in the treeline ecotone whereas young Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are nearly absent (MELLMANN-BROWN 2005). In the treeline ecotone on Niwot Ridge (Colorado Front Range) we found young growth of Engelmann spruce (73 %) to be more frequent than young growth of subalpine fir (9 %) and limber pine (*Pinus flexilis*, 18 %, HOLTMEIER 1999).

In the Swedish Scandes, during the last two to three decades,

the altitudinal limits of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) have advanced to greater elevation more rapidly than the mountain birch treeline (*Betula pubescens* ssp. *czerepanovii*; KULLMAN 2004, KULLMAN & ÖBERG 2009). Along transects reaching from the closed spruce-pine-birch-forest to the tree limit on Pallastunturi (807 m, western Central Finnish Lapland) seedlings and saplings of Norway spruce were by far more common than those of Scots pine and in particular of mountain birch (HOLTMEIER et al. 2003).

After-effects of human use

Not least, in many high mountains, warming climate and cessation of human impact as driving factors interfere in a complex and often elusive manner, in particular as site conditions in the formerly forested areas have often radically changed after the removal of the former high elevation forest stands. Thus, the alpine zone has become extended to lower elevations (cf. Fig. 1d) and the positive effects of climatic warming are overridden by the effects of a locally varying mosaic of strongly contrasting sites (Fig. 4). Lack of winter snow and dry conditions on convex and other wind-exposed topography as well as too long-lasting snow cover on lower leeward slopes and within shallow depressions may prevent or at least delay tree invasion into abandoned alpine pastures even although these are located below the present potential climatic tree limit and sufficient quantities of fertile seeds are available. At sites not or only episodically covered with snow, seedlings and saplings suffer from frost, winter desiccation

and abrasion by wind-driven ice and mineral particles while at sites covered with deep snow lingering into late spring or even early summer evergreen conifers may succumb to parasitic snow fungi such as *Herpotrichia juniperi*, *Phacidium infestans* and *Gremeniella abietina*. Particularly in winters with long-lasting wet snow fungi are very likely the most adverse factors for seedling survival. Also, mechanical damage caused to the young trees by creeping, sliding or settling snow may be fatal. Under current conditions, natural reforestation of abandoned alpine pastures in the Upper Engadine (Switzerland), for example, can be expected up to an altitude of 2300 m, while above this, growth rates and seedling density are insufficient (MÜTERTHIES 2002). In some areas, however, with less contrasting local topography, trees are invading in larger numbers abandoned or rarely used subalpine pastures.

The legacy of intense human use also influences secondary succession of tree species. When grazing pressure decreased grass and dwarf shrub vegetation could spread into patches where the mineral soil had been exposed by trampling effects of grazing cattle. The closed plant cover may now prevent the seeds of anemochoric tree species such as European larch (*Larix decidua*) for example from reaching a suitable seed bed or out-competes larch seedlings. In contrast, Swiss stone pine (*Pinus cembra*), which is normally the climax species in this area, has become a pioneer tree on abandoned alpine pastures due to the nutcracker's seed-caching activities. Inside pine clusters, the individual seedlings and saplings have greater protection from climatic injury than the more widely scattered pioneer trees such as larch.

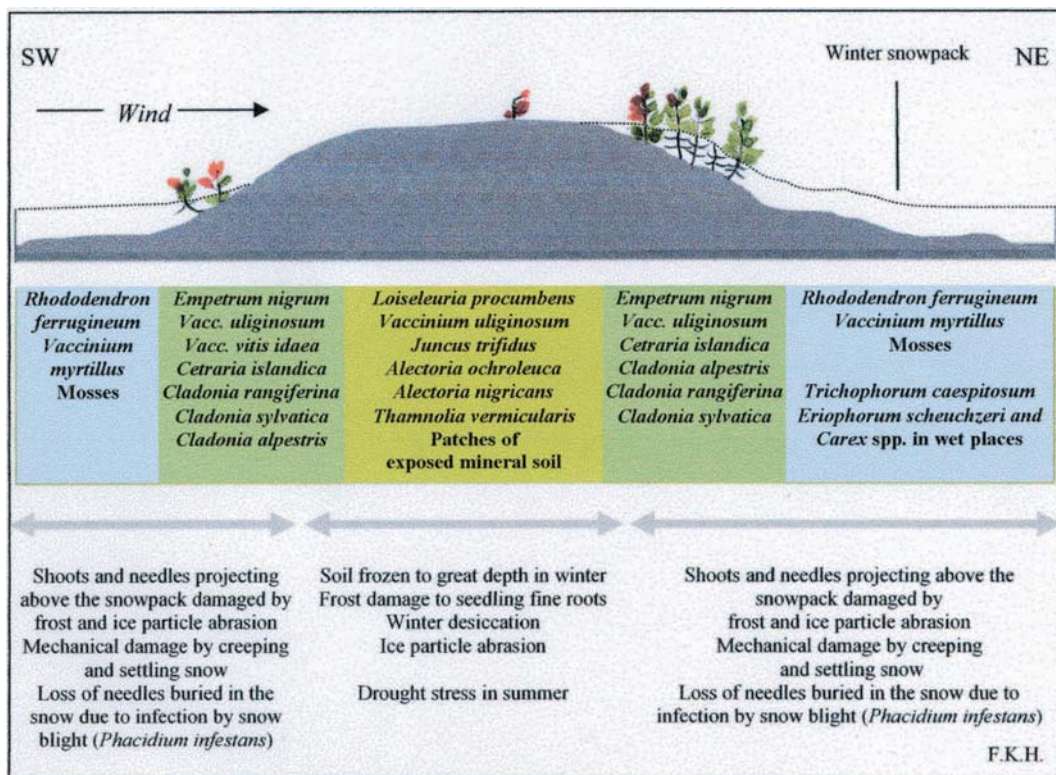


Fig. 4: Effects of local topography (exposure to solar radiation and wind) on site conditions and resultant distribution pattern of the ground vegetation and establishment of Swiss stone pine (*Pinus cembra*) in abandoned alpine pastures (schematic, following the conditions of the northwest-facing slope of the Upper Engadine main valley at about 2200 m). Modified from HOLTMEIER 1965.

Abb. 4: Auswirkungen der Geländegestalt (Strahlungs- und Windexposition) auf die Standortbedingungen, das Verteilungsmuster der Bodenvegetation und das Aufkommen von Arven (*Pinus cembra*) in aufgelassenen Alpweiden (schematisch, nach den Verhältnissen auf dem nordwest-exponierten Hang des Oberengadiner Haupttales, um 2200 m). Verändert nach HOLTMEIER 1965.

In many areas of the Alps as well as in the Low and High Tatra Mountains and in the Dinaric Alps, green alder (*Alnus viridis*) and prostrate mountain pine scrub (*Pinus mugo*) could expand after the removal of the original forest. These “true” krummholz species may impede or promote the establishment of spruce and other trees (e.g., ANTHELME et al. 2003, HOLTMEIER 2009). Such processes controlling secondary succession may be more important for the treeline pattern and dynamics than a warming climate (e.g., HOLTMEIER 1967, 1974, MÜTHERTHIES 2002, DULLINGER et al. 2003, 2004).

In northern Finnish Lapland, for example, it is the combination of excessive reindeer grazing and occasional mass-outbreaks of the leaf-eating autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) which pose a permanent threat to tree seedlings and young growth and act as agents for initiating or enforcing soil erosion (HOLTMEIER et al. 2004, HOLTMEIER & BROLL 2006, ANSCHLAG 2008).

The role of regeneration

Treeline shifts to higher elevation or more northern positions depend first of all on successful seed-based establishment of new tree generations in the alpine and northern tundra. Regeneration from seeds is a very sensitive process depending on several subsequent favourable growing seasons and is affected by a great number of external factors such as distance from the seed source, availability of a suitable seed bed, local climate, soil conditions, competition, mycorrhiza, nutrient availability, pathogens, allelopathic effects and irregular release of seeds from the cones (HOLTMEIER 1993, 2009). Seedling mortality is particularly high during the first years (e.g., MELLMANN-BROWN 2005, JUNTUNEN & NEUVONEN 2006).

The effect of the same factor on regeneration may be different in different locations. At the treeline in northern Sweden, for example, the establishment of mountain birch seedlings in the alpine tundra has been promoted by open patches of bare soil (TRUONG et al. 2007, SUNDQUIST et al. 2008). On the other hand, birch is apparently not able to invade wind-eroded

patches of mineral soil (sandy-skeletal till) on convex topography in the birch treeline in northernmost Finnish Lapland (Fig. 5) because of insufficient moisture and nutrient supply, adverse microclimate, and soil frost penetrating to great depth. At the treeline in Yukon Territory, it is black spruce (*Picea mariana*), which is not able to colonize open patches affected by cryoturbation (Fig. 6).

The position of the upper limit of regular viable seed production fluctuates in response to climatic conditions (Fig. 7). Under cool climatic conditions production of viable seeds and poor regeneration has been for a long time the bottleneck preventing tree advance to greater altitude and a more northern position. Transport of windborne seeds from distant seed sources at lower elevations or more southern forest stands has not been efficient enough to increase tree population at and beyond the existing tree limit during the last hundred years. In the treeline ecotone east of the Hudson Bay, for example, the abundance of spruce trees that originated from seeds decreases exponentially with latitude (GAMACHE & PAYETTE 2005). In the long-term the limit of production of viable seeds is located south (polar treeline) or below the physiological tree limit.

Some trees which originated from seeds during warmer conditions often far beyond the current northern and altitudinal tree limit have persisted by layering (formation of adventitious roots) for hundreds or even thousands of years without producing appreciable quantities of fertile seeds. Layering is still possible at temperatures too low for seed-based regeneration. It is common in deciduous trees but also occurs in some conifers. Long-lived clonal tree islands are very common at the altitudinal treeline in the Rocky Mountains and other high mountain ranges in western North America (Fig. 8), in Fennoscandia and in the Urals and also occur widely at the northern treeline in Eurasia and North America.



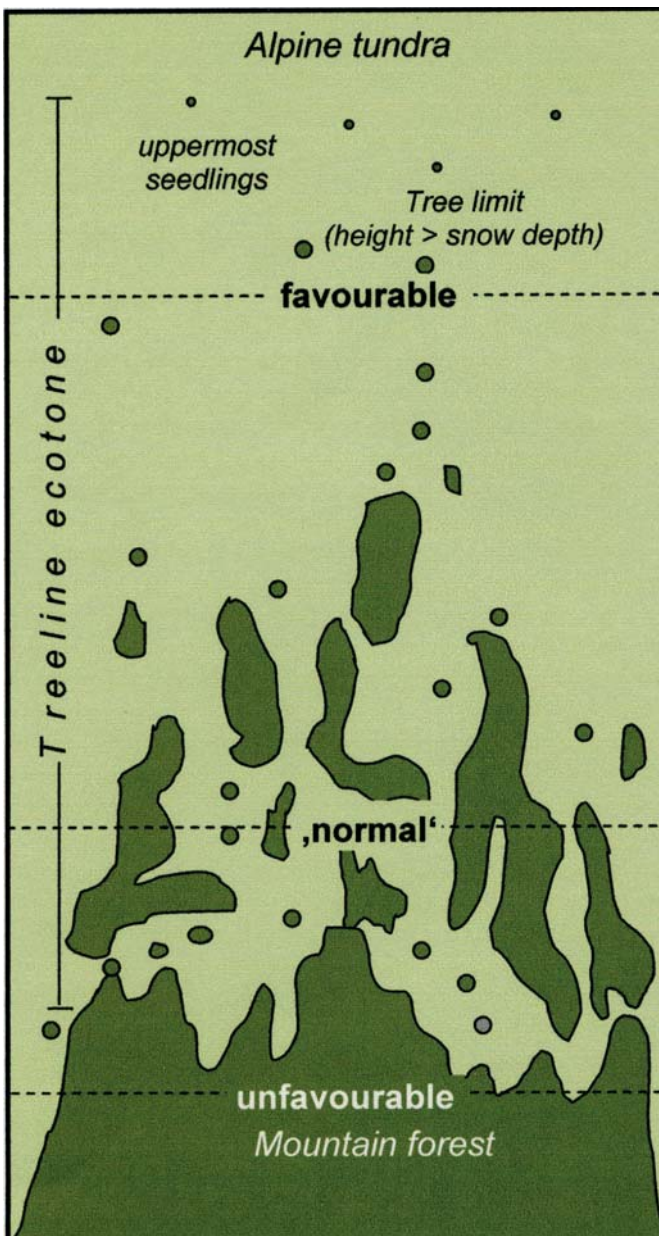
Fig. 5: Wind-eroded convex topography (327 m) on the northern slope of Koahppeloivi (northern Finnish Lapland). Lack of nutrients and soil moisture deficiency prevent mountain birch (*Betula pubescens* ssp. *czerepanovii*) from colonizing the eroded areas. Photo F.K.H., 26 July 1998.

Abb. 5: Winderodierte Kuppe (327 m) am Nordhang des Koahppeloivi (nördliches Finnisch Lapland). Nährstoff- und Feuchtemangel verhindern die Ansiedlung der Fjellbirke (*Betula pubescens* ssp. *czerepanovii*) auf den erodierten Flächen. Foto F.K.H., 26. Juli 1998.



Fig. 6: Treeline formed by black spruce (*Picea mariana*) near Dempster Highway (Yukon Territory) at about 640 m. Black spruce is absent from the open patches of mineral soil affected by cryoturbation. Photo G.B., 21 July 1993.

Abb. 6: Von der Schwarzfichte (*Picea mariana*) gebildete Baumgrenze in der Nähe des Dempster Highway (Yukon Territory) in ca. 640 m. Die Schwarzfichten können die durch Kryoturbation angehobenen Flecken offenen Mineralbodens nicht besiedeln. Foto G.B., 21. Juli 1993.



At most treelines, global warming is bringing about a change as the “new” trees that became established during the first decades and since the end of the 20th century within the upper zone of the treeline ecotone are now producing viable seeds. Seed dispersal by wind is however impeded as long as the pioneer trees do not project sufficiently beyond the surrounding vegetation. The situation will improve after the release of vertical stems, which can occur as a result of more favourable climatic conditions (cf. Figs. 8 and 11), especially if they reduce winter mortality. Also, ancient solitary trees and clonal tree groups that became established beyond the present forest limit during relatively favourable warm periods long ago may now become effective seed sources.

Feedbacks of trees and microsite facilitation

We are used to concentrating on the effects of increasing temperatures on treeline position and dynamics. However, the feedbacks of growing tree population within and beyond the treeline ecotone on their environment must also be considered (Fig. 9). They may even override the direct effect of the regional climates and climate warming.

Thus, infilling of the hitherto treeless patches in the treeline ecotone as well as the accelerated growth of young trees and release of vertical stems from already existing suppressed growth forms will reduce wind velocity and thus increase deposition of snow (cf. Fig. 8). A deeper snowpack will promote higher winter soil temperatures. Altered vegetation cover and higher soil temperatures accelerate mineralization and nutrient supply (e.g., more available nitrogen). As a result, biomass and productivity is likely to increase more than might be expected at the magnitude of direct effects of the warming climate (e.g., KAMMER et al. 2009).

Fig. 7: Position of the upper limit of production of fertile seeds at “normal”, favourable and unfavourable climatic conditions. Modified from HOLTMEIER 2009.

Abb. 7: Lage der oberen Grenze der Produktion keimfähiger Samen unter „normalen“, günstigen und ungünstigen klimatischen Bedingungen. Verändert nach HOLTMEIER 2009.



Fig. 8: Hedge-like clonal tree islands (*Abies lasiocarpa* and *Picea engelmannii*) on wind-swept terrain on Niwot Ridge (Colorado Front Range) at about 3450 m. Surface roughness and thus accumulation of blowing snow increased when climatic conditions more favourable than at present allowed some leaders to become upright stems. Photo F.K.H., 7 April 1989.

Abb. 8: Heckenartige Ablegergruppen (*Abies lasiocarpa* und *Picea engelmannii*) in windausgesetztem Gelände auf Niwot Ridge (Colorado Front Range) in 3450 m. Die unter günstigeren Klimabedingungen als heute zu aufrechten Stämmen herangewachsenen Wipfeltriebe haben die Oberflächenrauigkeit und infolgedessen die Schneeeinkummulation erhöht. Foto F.K.H., 7. April 1989.

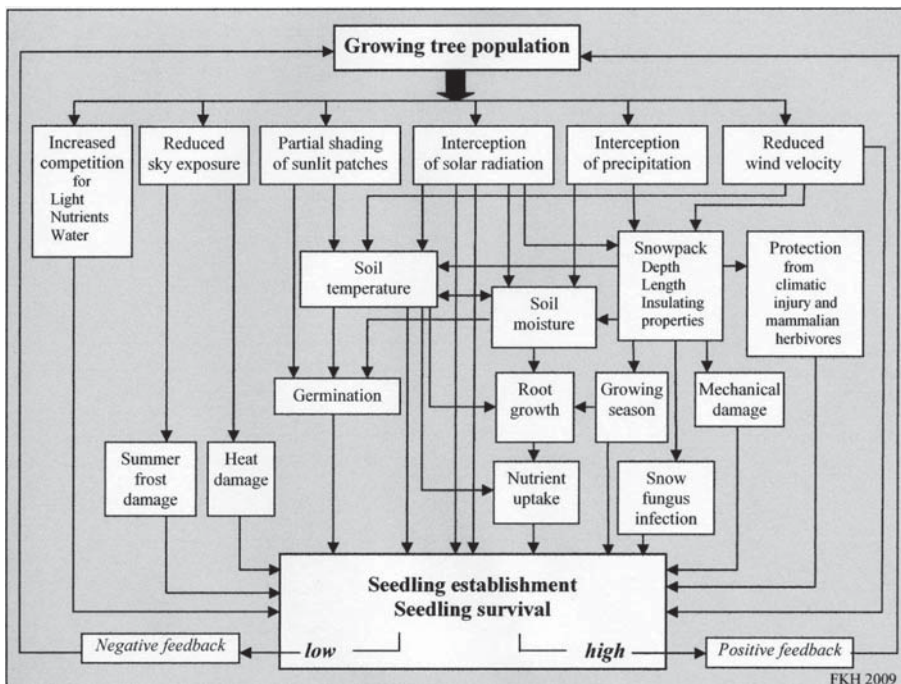


Fig. 9: Feedbacks of growing tree population on site conditions, seedling establishment and survival in the treeline ecotone. Modified from HOLTMEIER 2009.

Abb. 9: Rückwirkungen zunehmender Bestockungsdichte auf Standortbedingungen, Sämlingsaufkommen und Überlebensrate im Baumgrenzereich. Verändert nach HOLTMEIER 2009.

Moreover, a deeper snowpack may facilitate further seedling establishment. On wind-swept topography at the Rocky Mountain treeline, for example, compact clonal tree islands (cf. Fig.8) usually cause deep and long-lasting snow drifts at their leeward edge which provide shelter from climatic injury and, when melting, moisture supply to possible seedlings (MARR 1977, HOLTMEIER & BROLL 1992, BROLL & HOLTMEIER 1994). However, snow drifts lingering far into springtime or even early summer may also have negative effects because they promote parasitic snow fungi, which impair the successful establishment of potential seedlings.

In the Upper Engadine (Switzerland), for example, we found severe snow fungus damage within in open clusters of Swiss stone pine (*Pinus cembra*) on normally snow-free convex topography above the existing anthropogenic forest limit

(HOLTMEIER 1966). The taller growing pines have increased snow accumulation to an extent that younger and smaller specimens which germinated with a delay, were destroyed by snow blight (*Phacidium infestans*; Fig. 10).

Increasing tree populations not only provide shelter from strong winds but also from excessive solar radiation (e.g., GERMINO & SMITH 1999, GERMINO et al. 2002, JOHNSON et al. 2004, TAUSZ 2007). However, at higher tree densities shading of the ground by the tree canopy increases and may reduce soil temperatures and light intensity to an extent that germination of seeds and the establishment of seedlings of shade-intolerant tree species will be impaired or even prevented. It is unlikely however, that taller growing trees would eliminate themselves by shading the ground as has been argued by KÖRNER (1998a, 1998b).



Fig. 10: Swiss stone pines (*Pinus cembra*), which originated from seed caches of the European nutcracker (*Nucifraga caryocatactes*) on the northwest-facing slope of the Upper Engadine main valley at about 2200 m. The taller trees gradually increased snow deposition. They became affected by white snow blight (*Phacidium infestans*) and lost all their needles buried in the snowpack. The younger trees were completely destroyed. Photo F.K.H., September 1968.

Abb. 10: Aus Vorratsverstecken des Europäischen Tannenhähers (*Nucifraga caryocatactes*) hervorgegangene Arven (*Pinus cembra*) auf dem nordwestexponierten Hang des Oberengadiner Haupttales in 2200 m. Die heranwachsenden Bäume verursachten eine allmähliche Zunahme der Schneeeablagerung und wurden mit dem Schneeschüttepilz (*Phacidium infestans*) infiziert. Infolgedessen verloren sie alle ihre unter der Schneedecke begrabenen Nadeln. Die jüngeren Bäume wurden völlig zerstört. Foto F.K.H., September 1968.

In the alpine zone, seedling establishment is facilitated by boulders, solifluction lobes and terrace risers, hummocky surfaces, and shallow depressions that provide wind shelter and cause snow accumulation (HOLTMEIER 1965, 1974. ALFTINE & MALANSON 2004, BUTLER et al. 2004, RESLER 2006, BATLLORI & GUTIÉRREZ 2009). Shrubs (e.g. willows) or grass tussocks may have a similar effect. Varying microtopography (rough ground surface) might be more favourable than smooth terrain (HOLTMEIER et al. 2003). In addition, already existing suppressed growth forms (e.g., mat and table growth) or dead “krummholz” may support the establishment of new seedlings in a similar way (Fig. 11; see also. BEKKER 2005).



Fig. 11: Three young subalpine fir (*Abies lasiocarpa*) and a lodgepole pine (*Pinus contorta*) have become established in the lee of a clonal group of subalpine fir on this wind-swept site on Lee Ridge (Glacier National Park, Montana) at about 2000 m. The clonal group and its leeward snow-drift which builds up in winter provide shelter from the strong winds to the young trees. After a field sketch by F.K.H., 2009.

Abb. 11: Drei junge subalpine Tannen (*Abies lasiocarpa*) und eine Drehkiefer (*Pinus contorta*) sind im Lee einer Tannen-Ablegergruppe an diesem windgefegten Standort auf dem Lee Ridge (Glacier Nationalpark, Montana) in ca. 2000 m Höhe aufgekommen. Die Ablegergruppe und der im Winter auf ihrer Leeseite abgelagerte Schnee bieten den jungen Bäumen Schutz vor den starken Winden. Nach einer Feldskizze von F.K.H., 2009.

Despite positive feedbacks of increasing tree populations, microsite facilitation and climate warming most of the trees which became established above the upper forest stands during the last decades have not been able to develop normal growth. In northernmost Finnish Lapland, for example, more than 80 % of living Scots pines (*Pinus sylvestris*), which established themselves within and beyond the birch-treeline ecotone after the 1970s show moderately to severely disturbed growth (HOLTMEIER & BROLL submitted). Others have already died. Similar observations we made at the treeline in Ounas-Pallastunturi-National Park (western central Finnish Lapland; HOLTMEIER et al. 2003) and throughout the Rocky Mountains (HOLTMEIER 2009). NINOT et al. (2008) suppose that vertical growth of pine (*Pinus uncinata*) at treeline in the Catalan Pyrenees may be prevented by climatic impact for decades at least.

Also in a warmer environment distorted growth forms will prevail close to the future higher tree limit as it was the “rule” also in the past. Many of the trees may survive for decades as suppressed growth forms. During a series of favourable years height growth may accelerate and the trees will attain “tree size” provided this is not prevented by extreme events such as exceptionally cool summers, extremely cold and snow-poor winters or relatively mild winters with deep and long-lasting snow pack.

Adverse effects of climatic warming in the treeline environment and biodiversity concerns

Although the many positive effects of climatic warming on treeline are obvious, future opposite effects cannot be excluded. Thus, at the northern treeline summer drought is likely to become an adverse factor (e.g., BRIFFA et al. 1998, BARBER et al. 2000, GAMACHE & PAYETTE 2005, WILMKING et al. 2004, 2005), at least locally. At the treeline in Alaska, for example, tree growth decreased on warm and dry sites after the 1950s, possibly because of drought stress (LLOYD & FASTIE 2002). In the Kenai Mountains, where seedlings became established at relatively great numbers up to 100 m above the existing “krummholz” particularly during the period 1975-1995, seedling establishment decreased during the last decade which was hotter and drier than the two decades before. Tree-line rose only on cooler northern aspects by about 50 m in less than 50 years (DIAL et al. 2007). Moisture stress is most critical at the seedling stage and would occur first on highly permeable and rapidly drying substrates such as sandy-skeletal soils (cf. Fig. 5; HOLTMEIER et al. 2003, HOLTMEIER & BROLL

2005). However, seedlings that established themselves on moss layers may also suffer from insufficient moisture supply after the moss layer has dried and the seedling roots have not reached the mineral soil (KINNAIRD 1974, HILLE & OUDEN 2004). Also, at the upper treeline in temperate high mountains dry conditions may occur more frequently during the growing season and affect seedlings and young growth. At the upper treeline in the Italian Central Alps, for example, decreasing sensitivity of radial growth in Swiss stone pine (*Pinus cembra*) on south- and southwest-facing sites to summer temperature and increasing sensitivity to July temperature on northern aspects (LEONELLI et al. 2009) suggest a temperature-induced drought stress on the sun-exposed sites. Increasing temperature and decreasing precipitation as predicted by IPPC (2007) for southern Europe might cause widespread drought stress at the treeline in the Mediterranean (e.g. CAMARERO & GUTIÉRREZ 2004, BRANDES 2007, BATLLORI 2008). Drought stress to seedlings is more likely on sun-exposed leeward slopes than on sun-exposed windward slopes. In continental climates, hot and dry summers are likely to become a serious threat to seedlings in the treeline ecotone, particularly on southern aspects, while warm and wet summers will promote seedling establishment.

Drought due to climate warming is likely also to increase fires, which will not only destroy tree stands but also the soil organic layer. The remains will rapidly erode under the influence of surface-runoff and wind (Fig. 12). The loss of the organic layer will have a long-lasting effect as it is the main nutrient source. As a result treeline post-fire regeneration will be delayed or even be absent for decades or even longer.

Moreover, winter warming (ACIA 2005) will bring about more wet snow. Increasing crown and stem breakage due to heavy snow loads as well as damage caused by settling snow are likely. More wet snow, particularly in springtime, will increase the risk of young growth of evergreen conifers becoming infected by parasitic snow fungi. Moreover, seedlings and saplings would be affected by mechanical damage. As a result, treeline advance may locally be delayed.

Tree line advancing to greater altitude and more northern position is supposed to bring about fragmentation of the alpine and

tundra vegetation, loss of species and biological diversity (e.g., LUCKMAN & KAVANAGH 2000, THEURILLAT & GUIBAN 2001, MALANSON et al. 2007, SUNDQVIST et al. 2008). Simulated changes of the future position of the upper treeline in Sweden suggest a reduction of alpine heaths by about 80 %. The rest would be slope debris and boulder fields (MOEN et al. 2004). KULLMAN (2007) objects emphatically to this hypothesis as field observations do not support it. The risk of species extinction may possibly be reduced by survival of many alpine species on cliffs and slopes too steep for closed forests as it happened in the past (BRUUN & MOEN 2003). Forest altitudinal advance will however reduce landscape diversity, which would impair the landscape aesthetic values and make the landscape less attractive for tourists. This would considerably affect the economy in the Alps and in other mountains, which are similarly dependent on tourism.

At the northern treeline, increasing tree populations may influence the interactions between tree cover and thaw depth of permafrost (e.g., KRYUCHKOV 1973, LARSEN 1989, HOLTMEIER 2009) and thereby the spatial and temporal treeline patterns. In subarctic lowland areas, as western in Siberian and in the Hudson Bay region for example, melting permafrost and resultant paludification are likely to cause a retreat of the northern forest where topography and drainage control the extent and rate of paludification (CRAWFORD et al. 2003, SIMARD et al. 2007).

Forest advance would also increase insect harassment and reduce the open wind-swept areas frequented by reindeer to escape molestation by nose bot flies (*Cephenemyia trompe* L.) and warble flies (*Hypoderma tarandi* L.). As a result reindeer impact on these areas will be likely to increase.

Topographical control of treeline dynamics

A general rise of treeline, which could be expected under persistent warmer conditions is considerably modulated by the effects of geomorphic structures on the site conditions. The topographically determined basic spatial pattern in the treeline ecotone will probably not change significantly under the influence of climatic change (HOLTMEIER & BROLL 2005).



Fig. 12: A wildfire destroyed this "krummholz" stand in 1988 near Coney Lake (Front Range, Colorado, at about 3250 m). Afterwards, run-off and strong winds have eroded the organic layer, which was the main nutrient source. Photo F.K.H., 6 August 1989.

Abb. 12: Ein Feuer zerstörte 1988 diesen „Krummholzbestand“ in der Nähe von Coney Lake (Front Range, Colorado, bei ca. 3250 m). Danach haben Abspülung und starke Winde die organische Auflage und damit die wichtigste Nährstoffquelle zerstört. Foto F.K.H., 6. August 1989.

The extent of any climate-induced movement of the treeline ecotone will vary with the angle of incline. Put simply, on a gentle slope the treeline will move further than on a steep slope (Fig. 13). On steep valley sides, climate warming is unlikely to make the forest advance to its rising climatic potential limit as long as gravitational processes (cf. Fig. 1e) regularly occur at intervals (AUTIO & COLPAERT 2005, HOLTMEIER & BROLL 2005, 2007). In the long-term trees may become established after the block debris has stabilized and fine mineral and organic material accumulated which improves moisture and nutrient conditions. Persistent invasion of active avalanche chutes by arborescent vegetation is unlikely in particular as in a warmer climate more snow will probably accumulate above the present high altitude forest where most of destructive avalanches are released (BENISTON 2001, BEKKER et al. 2007). Thus, on slopes intensively dissected by erosion and showing a rib-and groove topography, forest expansion to greater elevation will follow the rib structures while advance will be delayed or prevented in the rills and gullies which are usually identical with avalanche pathways.

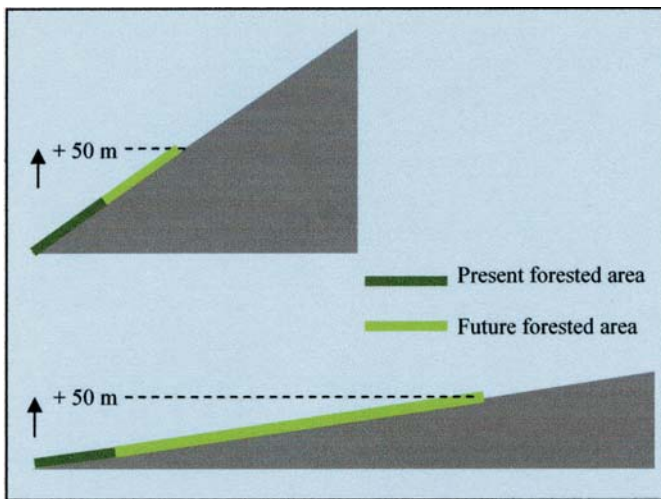


Fig. 13: Possible increase of the forested area caused by a climatically driven upward shift (e.g., by 50 m) of the treeline ecotone varies with slope inclination.

Abb. 13: Die mögliche Zunahme der bewaldeten Fläche infolge eines klimatisch verursachten Anstiegs der Baumgrenze (z.B. um 50 m) variiert mit der Hangneigung.

The situation is completely different on gentle slopes and rolling plains as for example on uplifted often smooth old land surfaces in the Rocky Mountains or in Finnish Lapland. As a result of warming new trees have established themselves mainly in places that are sufficiently but not too long covered with snow; i.e. at the lee side of convex topography (e.g., hillocks, eskers, terminal moraines) and alongside the upper rim of shallow valleys and other depressions. In general, tree invasion has been less successful on top of windswept topography. Locally however, facilitation by stones, grass tufts, dwarf-shrub patches and shallow depressions not exceeding a few centimetres in depth has been sufficient for seedlings establishment during the last decades. In the Colorado Rocky Mountains, for example, seedlings can be found in places up to altitudes of 3600 m. However, up until now they have not developed normal growth because of the extremely windy conditions. In the lower slope zone of convexities and on the

floor of shallow valleys as well as along stream sides where winter snow may linger into early summer evergreen conifers are rare, mainly because of being infected by snow fungus. Also waterlogging may prevent tree establishment in such places. In northernmost Finnish Lapland, however, we found mountain birch (*Betula pubescens* ssp. *czerepanovii*) expanding to higher elevation mainly within the shallow valleys cut into sandy-skeletal basal till (HOLTMEIER et al. 2003, BROLL et al. 2007).

IMPLICATIONS

Climate warming since the end of the Little Ice Age has encouraged tree establishment within the treeline ecotone and above the upper tree limit. Increase of tree population in the treeline ecotone and migration of the tree limit to a higher elevation and a more northern position is ubiquitous with regional and local exceptions however. In most areas, tree recruitment has been most intense within the treeline ecotone while above trees are still sporadic. The utmost pioneer trees will probably survive for decades as suppressed growth forms until a succession of favourable years would allow accelerated height growth and provide no setbacks from extreme climatic events, pathogens, diseases or insect infestations. Extreme events are however almost unpredictable. In continental climates treeline shift is more likely under warm and humid conditions than under warming alone.

As long as low temperatures limit carbon investment, enriched CO₂ in the atmosphere and increasing carbon assimilation are unlikely to promote tree growth and treeline advance to higher elevations or more northerly positions. Nevertheless, it is to be expected that different tree species may respond differently (e.g., HANDA et al. 2005).

One may safely assume that in the case of continued warming and stabilization of the thermal conditions at a higher level than at present advancing treelines will bring about a profound landscape change in high mountains and at the southern rim of the Arctic. The feedbacks of the growing tree population within and beyond the treeline ecotone are likely to play an important role in this respect. Absence of microsite facilitation would delay or even prevent treeline rise driven by the warming climate.

Regional and local variation will occur because of historical legacies (Fig. 14), different climates (climate character), landforms, pathogens, diseases, etc. Moreover, the tree line does not and will not advance in a closed front to higher elevations or more northern positions as varying microtopography controls site conditions and tree establishment. Focussing on thermal conditions only, in order to set up a generalized hypothesis, would ignore the regionally and locally varying response of the upper and northern treelines spatial and temporal patterns to the changing environment. At the landscape and local scales the role of wild-living animal populations should not be disregarded.

Whereas little imagination is needed to predict that in case of persistently higher temperatures treelines will move upwards and to a more northern position, probably up to its maximum in the Early Holocene (MACDONALD et al. 2008), it is however

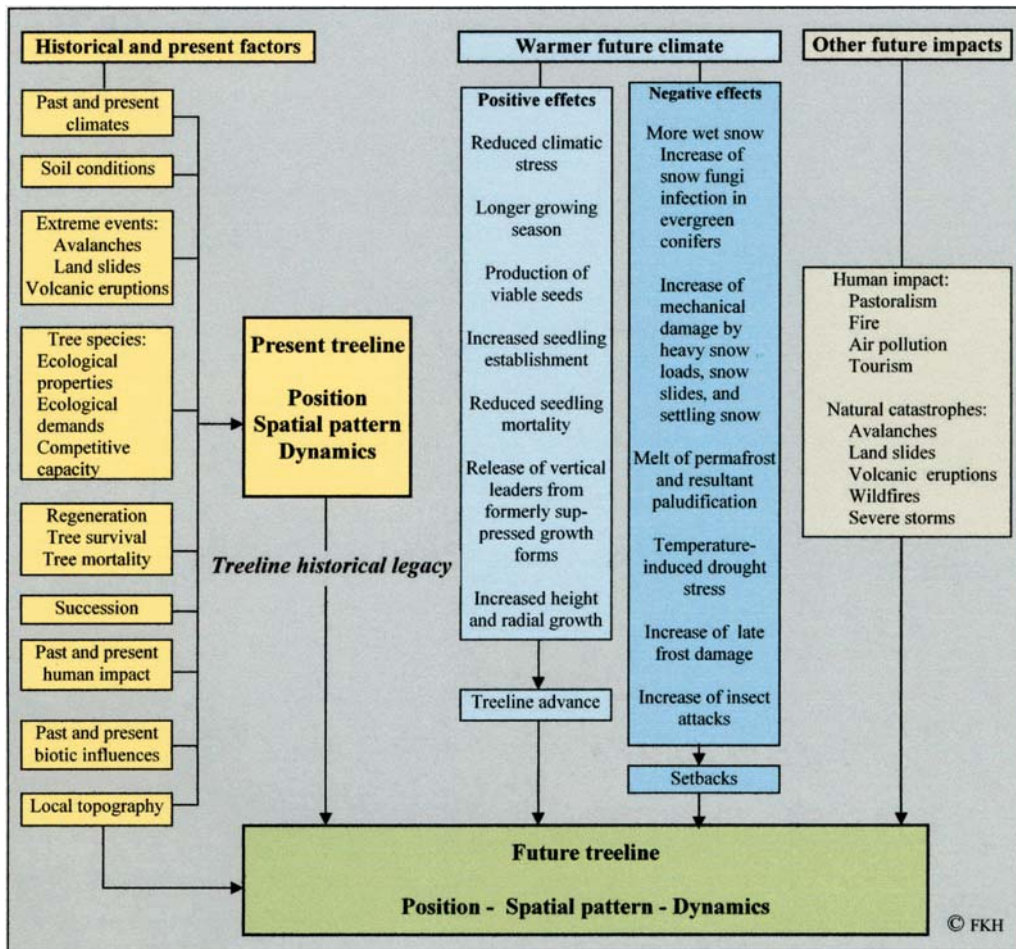


Fig. 14: The influence of treeline historical legacy, climate warming and some other factors on the position, spatial pattern and dynamics of the future tree line. Modified from HOLTMEIER & BROLL 2005.

Abb. 14: Der Einfluss der Baumgrenzgeschichte, der Erwärmung und einiger anderer Faktoren auf Lage, räumliche Struktur und Dynamik der künftigen Baumgrenze. Verändert nach HOLTMEIER & BROLL 2005.

much more difficult to predict regional and local variations and dynamics of treelines. More regional and local studies are urgently needed. In setting up hypotheses on the future tree line development we rely on what we know about the present and past relationships between climatic variables, tree growth, adaptation to rising temperatures, seedling performance and intraspecific and interspecific competition for example. However, we cannot be sure whether these relationships will be the same in a generally warmer climate.

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