



Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales

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ABSTRACT

The sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change are increasingly discussed in terms of climate change, often forgetting that climate is only one aspect of environmental variation. As treeline heterogeneity increases from global to regional and smaller scales, assessment of treeline sensitivity at the landscape and local scales requires a more complex approach than at the global scale. The time scale (short-, medium-, long-term) also plays an important role when considering treeline sensitivity. The sensitivity of the treeline to a changing environment varies among different types of treeline. Treelines controlled mainly by orographic influences are not very susceptible to the effects of warming climates. Greatest sensitivity can be expected in anthropogenic treelines after the cessation of human activity. However, tree invasion into former forested areas above the anthropogenic forest limit is controlled by site conditions, and in particular, by microclimates and soils. Apart from changes in tree physiognomy, the spontaneous advance of young growth of forest-forming tree species into present treeless areas within the treeline ecotone and beyond the tree limit is considered to be the best indicator of treeline sensitivity to environmental change. The sensitivity of climatic treelines to climate warming varies both in the local and regional topographical conditions. Furthermore, treeline history and its after-effects also play an important role. The sensitivity of treelines to changes in given factors (e.g. winter snow pack, soil moisture, temperature, evaporation, etc.) may vary among areas with differing climatic characteristics. In general, forest will not advance in a closed front but will follow sites that became more favourable to tree establishment under the changed climatic conditions.

Keywords

Anthropogenic treeline, climatic treeline, environmental change, orographic treeline, sensitivity, regeneration, treeline dynamics, treeline ecotone, treeline physiognomy.

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INTRODUCTION

As the location of northern hemisphere altitudinal and polar treelines are caused mainly by heat deficiency, global warming is expected to cause treelines to advance to higher elevations and more northerly latitudes (e.g. Kauppi & Posch, 1988; Westman *et al.*, 1990; Ozenda & Borel, 1991; Gates, 1993; Neilson & Chaney, 1997; Batchelet & Neilson, 2000; Rupp *et al.*, 2000; Grace *et al.*, 2002). The future position of the upper and northern treelines, which is considered to be an indicator of the effect of changing environment, is increasingly discussed at an international level (e.g. Programme Advisory Committee, 1999; Callaghan *et al.*, 2002). However, climate change is only

one aspect of environmental change that may affect the location of treelines.

In this present paper, the term 'treeline' is applied to the transition zone extending from closed subalpine or northern forests to the uppermost or northernmost usually scattered and stunted individuals of the forest-forming tree species — regardless of their height (Holtmeier, 1981, 2003). The upper or northern limit of the treeline ecotone is called the tree-limit.

The sensitivity of treelines to environmental change implies a certain state of readiness of the trees to respond to changing conditions. This can take place by changes in growth, growth forms, regeneration and treeline structures (spatial structures, mosaics), and can also be related to changes in alpine or tundra vegetation,

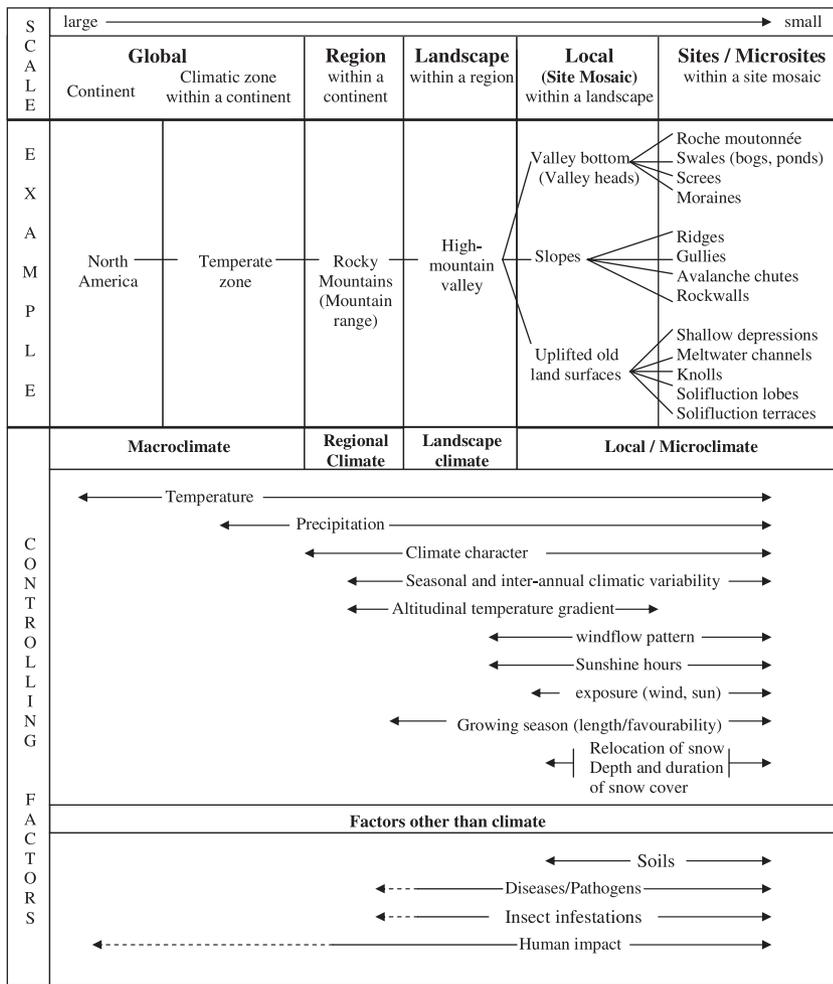


Figure 1 Treeline-controlling factors at different scales. Treeline heterogeneity increases from the global to smaller scales.

age classes and distribution pattern of plant communities. Sensitivity is great where even the slightest change in a limiting factor is followed by prompt response in tree growth and treeline patchiness.

The treeline is a space- and time-related phenomenon. When assessing treeline sensitivity and its potential response to changing environmental conditions, spatial scale plays an important role (Fig. 1). At the global scale, even the relatively broad forest–tundra boundary is reduced to a ‘line’ snaking for about 13,000 km along the northern rim of Eurasia and North America. This ‘line’, defined by a certain coverage (e.g. 30% or 40%), can be mapped from satellite images or other remote sensing techniques (Rees *et al.*, 2002) and correlated to isolines of temperature (e.g. mean temperature of the warmest month or of three or four warmest months, growing degree-days, etc.; see critical review in Tuhkanen, 1980). At this scale, a northern treeline advancing parallel to the northward shift of a ‘treeline-controlling’ isotherm would reflect a high treeline sensitivity. However, this theoretical treeline should not be considered like an organism responding to its changing environment. It has become evident from regional treeline studies that position and structure rarely change in parallel to the shift of any isotherm. Nor do treelines shift synchronously with climatic change (Holtmeier, 1995, 2003;

Holtmeier *et al.*, 2003). Moreover, the factors controlling treeline structures are strongly scale-dependent (e.g. Kupfer & Cairns, 1996).

At the landscape scale, treeline varies widely because of the given regional and local geomorphologies, and the fragmented nature and ecotonal character of the treeline become obvious. Even comparatively narrow altitudinal treelines are usually characterized by mosaics of habitats. The ecological conditions within this transition zone are totally different from the mountain or from boreal forest and from the alpine zone or northern tundra (Fig. 2).

Treeline heterogeneity increases from the global to the regional, landscape and local scales (Fig. 1). Thus, assessment of treeline response to changing environment (climate) at the regional and smaller scales requires a much more complex approach than at the global scale (e.g. Körner & Paulsen, 2004). From the landscape-ecological point of view, there is no scientific justification for relating treeline position at this scale with only one factor such as mean air or soil temperature (e.g. Körner, 1998a,b, 2003). Instead, many factors must be considered. These factors control the present position and spatial structure of the treeline ecotone, which also reflect the influence of climate history, vegetation history and historical human impact (Fig. 3). Thus, present conditions reflect treeline history and influence

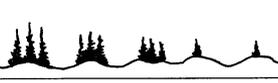
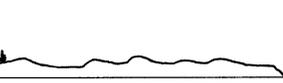
Forest	Treeline ecotone	Alpine/Tundra
		
Radiation transfer in the upper canopy layer	Radiation transfer at the surface of the alpine vegetation, of tree clumps and at the soil surface	Radiation transfer at the surface of the alpine vegetation and at the soil surface
Almost no influence of microtopography on insolation	Insolation strongly influenced by microtopography and tree clumps	Insolation strongly influenced by microtopography
Almost no effect of microtopography on wind velocity and direction	Wind velocity and direction strongly influenced by microtopography and tree clumps	Wind velocity and wind direction strongly influenced by microtopography
Low wind velocity	High wind velocity	High wind velocity
High interception of precipitation by the forest canopy	Interception of precipitation by scattered tree clumps and alpine vegetation	Interception of precipitation by alpine vegetation
Relatively even depth and duration of snowpack	Widely and locally varying depth and duration of snowpack due to the influence of the mosaic of tree clumps and alpine vegetation	Widely and locally varying depth and duration of snowpack due to the influence of microtopography
High humidity and relatively even distribution of soil moisture	Very locally varying humidity and soil moisture	Very locally varying humidity and soil moisture
'Forest soils' (in conifer forests mainly podzols)	Mosaic of different soils controlled by microtopography and tree clumps	Mosaic of different soils controlled by microtopography

Figure 2 Ecological characteristics of forest, treeline ecotone and alpine or northern tundra.

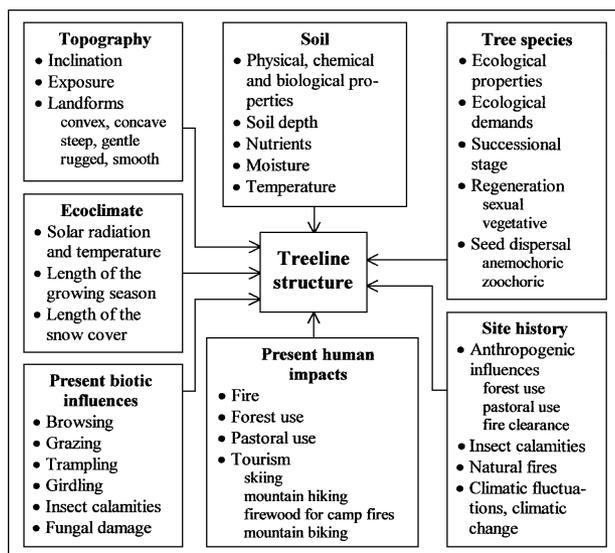


Figure 3 Factors influencing spatial and physiognomic treeline structures (modified from Holtmeier, 2003).

future changes (Holtmeier, 2000, 2003; Payette *et al.*, 2001). They may even override the effects of a general warming on treeline sensitivity and response.

In addition to spatial scales, time-scale plays an important role in assessing treeline sensitivity to changing environments. Short-term response, defined as a year or less, is reflected in individual trees (Table 1). Medium-term response (some years to a few decades) is mirrored in changing tree physiognomy (phenotypical response), tree-ring width and density, survival rate in seedlings and young trees, successional stage of the plant cover, etc. Tree-ring patterns also help to improve our understanding of site history, particularly if supported by radiocarbon dating of wood remains. Tree rings, however, do not allow prediction of future development. Medium-term and long-term responses (several decades to one hundred or more years) may be simulated by scenarios based on the projection of the present empirical relationships between treeline and environmental factors into a warmer future environment. However, we do not really know whether the present more or less well-documented interrelationships of the many tree-affecting factors and their relative intensity will be the same in a warmer climate (see also Giorgi & Hewitson, 2001).

Table 1 Treeline response to changing environment at different time-scales

Short-term response of individual trees (≤ 1 year)	Medium-term response of tree stands/forests (some years to several decades)	Long-term response of tree stands/forest (several decades to hundreds of years)
Photosynthesis Carbon allocation Period of shoot extension	Changing tree physiognomy Production of viable seeds Successful establishment of trees	Forest advance (or retreat) Tree limit advance (or retreat) Feedbacks of increasing forest cover on the regional and local climates (snow cover, albedo)
Date of needle flush Annual height and radial growth Maturation of newly formed tissue Ripening of seeds	Effects of increasing tree coverage on microclimates and vegetation in the understory (competition, succession)	

SENSITIVITY AND RESPONSE IN DIFFERENT TREELINE TYPES

The response of treelines to changing environmental conditions varies among orographic, anthropogenic or climatically determined treelines.

Orographic and edaphic treelines

Orographic treelines occur commonly in mountainous areas. Steep rock walls, slope debris, boulder scree, talus cones and avalanche chutes may limit the forest at relatively low elevation, whereas solitary trees and tree groves may occur far above at sites protected from wasting and avalanches. In cases where orographic factors prevent forest establishment, warmer climate will not cause an advance to a greater elevation as long as mass-wasting, debris slides, etc., occur. Consequently, the spatial distribution of trees and tree groves is stable and is likely to remain so. Eventually, trees may invade stable block debris when sufficient fine material and organic matter have accumulated between the blocks. Avalanche chutes may also be temporarily invaded by forest if avalanches do not occur too frequently. In view of general warming, however, persistent establishment of forest at such sites seems unlikely as the vapour content of the atmosphere will increase (e.g. Folland & Karl, 2001) and may cause greater snow accumulation at high altitudes (Beniston, 2001). If warming should curtail the annual period of avalanche activity, this would not necessarily result in a decreasing number of destructive avalanches because they are usually released by extreme weather conditions lasting only a few days (Bader & Kunz, 1998).

In mountain areas, other than volcanoes, edaphic treelines are usually limited in space and often hard to distinguish from orographic treelines. On boulder scree, for example, unstable and moving slope debris and lack of soil moisture and nutrients may prevent trees from invading such sites. In the northern treeline ecotone, the situation is different. Waterlogging and paludification often cover wide areas, particularly on gently sculptured old land surfaces. Convex, well-drained topography may be too dry for seedling establishment. Thus, the northern treeline often

depends more on climate and soil conditions than on orographic factors (see also Tanfiljew, 1911; Blüthgen, 1942).

On volcanoes, treeline advance to higher altitude will primarily be controlled by edaphic conditions rather than by a warming climate. Lack of moisture as well as the high-altitude climate may considerably delay pedogenesis (Grishin *et al.*, 1996) and establishment of tree seedlings (e.g. Veblen *et al.*, 1977; Daniels & Veblen, 2004). However, where soil moisture increases due to organic matter accumulation in the upper layers, soil development and plant invasion will accelerate (Grishin & Del Moral, 1996). Consequently, the treeline is likely to become more sensitive to a warming climate.

Anthropogenic treelines

Even in remote northern regions, little remains of untouched nature (e.g. Holtmeier, 1974, 2003; Holtmeier *et al.*, 2003; Emanuelsson, 1987; Haapasaari, 1988; Hofgaard, 1997a,b, 1999;). In mountainous regions such as the European Alps or the Norwegian Fjordland, human use has been topographically limited to accessible areas such as trough shoulders and similar relatively gentle terrains on the mountain slopes. Consequently, treeline was lowered. A depression of 150 m to 300 m can be accepted as an average value. At present, the altitudinal limit of tree growth is located above the man-caused forest limit (e.g. Holtmeier, 1974, 1993b, 1994a,b, 2003; Slatyer & Noble, 1992; Thimon, 1992; Tessier *et al.*, 1993; Burga & Perret, 2001).

In many areas, the aspect of the anthropogenic treeline ecotone has changed during the recent decades (e.g. Holtmeier, 1965, 1967a,b, 1974, 2003; Spatz *et al.*, 1978; Weis *et al.*, 1982; Nola, 1994; Mütterthies, 2002) and appears likely to change in the future. Spontaneous invasion of seedlings and young growth into almost treeless areas above the anthropogenic forest limit, and the changing physiognomy of scattered and hitherto environmentally suppressed trees in the treeline ecotone, are often readily ascribed to the effects of warming climates. It is already evident that strong warming signals have occurred in the Alps since the 1980s (Beniston, 2001). The upward shift of the distribution limit of plant species in the alpine and subalpine belt reported for some regions in the Alps and Scandinavia may also

be taken as an indicator of climate warming (Burga & Perret, 2001; Theurillat & Guisan, 2001; Burga *et al.*, 2003; Walther, 2003; Walther *et al.*, 2005). However, on-going observations suggest that changes in the European Alps, in the Norwegian Fjordland and in the Cairngorm Mountains of Scotland, for example, are triggered mainly by cessation of human impact (mainly pastoral use and mining) rather than by climatic warming (Holtmeier, 1974, 1994a,b, 2003; Oksanen *et al.*, 1995; Aas & Faarlund, 1996; French *et al.*, 1997; Stützer, 2000, 2002; Bryn & Daugstad, 2001; Mütterthies, 2002, 2003).

The supply of viable seeds has never been a problem in anthropogenic treelines because the distance from seed sources in the remaining mountain forest at lower elevations is usually relatively short (in contrast to undisturbed climatic treelines). Although tree seedlings may occur at great numbers after cessation of pastoral use, trees invading former pastures are often impeded more by unfavourable site conditions than might be expected in low level forests under a warming climate. The anthropogenic treeline has therefore become an ecological boundary sensitive to climate just as formerly the natural climatic treeline had been in the past (Holtmeier, 1965, 1974, 1990). Site conditions, particularly microclimates, can change radically after the removal of the former forest. Wind flow and the amount of solar radiation near the soil surface are both strongly influenced by local topography. Sites vary in their exposure to solar radiation, wind velocity and direction, depth and duration of the winter snow cover, soil moisture, soil temperatures and other factors. With slightly warmer climatic conditions, strongly contrasting site conditions are likely to control the advance of tree growth to higher elevations in the same way as in the undisturbed treeline ecotone (cf. Climatic treelines). Tree invasion usually follows on suitable sites, particularly on areas with convex topography and not too long-lasting snow cover, where they may have already reached their present potential climatic limit. The variegated topography and its influence on site conditions causes an irregular mosaic of forest patches and results in more or less scattered tree groves separated by alpine meadows and dwarf-shrub vegetation.

As has become evident from recent studies on the natural reforestation of abandoned alpine pastures by *Larix decidua* and *Pinus cembra* in the Upper Engadine (Switzerland), effective establishment of trees can be expected up to an elevation of 2300 m (potential treeline), while above this, seedling density and growth rates are insufficient for natural reforestation (Mütterthies, 2002, 2003). Thus, under these particular conditions, trees are not likely to advance to the historical maximum position of the upper limit of tree growth, although sensitivity to the changing environment is high. Obviously, the potential effect of warming climate is reduced by the after-effects of historical forest removal. However, this may change if climate warming continues.

In northern Finnish Lapland, where the mountain birch treeline declined over wide areas as a result of excessive grazing by reindeer and of mass outbreaks of the autumnal moth (*Epirrita autumnata*), natural invasion of mountain birch into almost treeless areas in the treeline ecotone (Fig. 4) is also impeded by



Figure 4 View from the north on the east-facing slope of Koahppeloivi (northernmost Finnish Lapland). After the decline of the mountain birch forest (*Betula pubescens* spp. *czerepanovii*) due to mass outbreaks of the autumnal moth (*Epirrita autumnata*) and overgrazing by reindeer, convex topography became eroded by wind. The photograph was taken from about 300 m above ground. — Photograph taken by F.-K. Holtmeier, 5 August 1998.

adverse microsite conditions resulting from historical human impact, present herding practices and intense soil erosion (Kumpula & Nieminen, 1992; Helle & Kajala, 1993; Käyhkö & Pellikka, 1994; Evans, 1995; Lehtonen & Heikkinen, 1995; Neuvonen *et al.*, 1996, 2001; Broll, 2000; Holtmeier, 2002, 2003; Holtmeier *et al.*, 2003).

Climatic treelines

Climatic limits of tree growth will occur only if no other factors, such as orography or human impact, prevent tree growth from reaching its climatically caused altitudinal or northern limit. At the landscape and local scales, other factors such as soil moisture or soil temperature, for example, and their side-effects influence treeline simultaneously and interact with climate. Moreover, site history, including climatic changes, wildfires, human impact, insect infestations and plant diseases play a very important role and have to be considered at the landscape scale when discussing sensitivity of the so-called climatic treeline to changing climate.

Heat deficiency is a very complex factor. It depends not only on the decrease of temperature with altitude and latitude but also on wind (cooling effect), length of the winter snow cover, soil moisture and seasonal temperature differences. Wind flow pattern and wind velocity near the ground in the treeline ecotone are controlled by the local topography and by the influence of the mosaic of tree stands and treeless spaces (Fig. 2; Holtmeier, 1996, 2003). The amount of solar radiation is modified by slope aspect (exposure), horizon elevation angle, microtopography and vegetation (e.g. shading by mature trees or forest understory; Smith *et al.*, 2003). Moreover, interannual temperature variability is an important factor. In highly variable areas, for example, the probability of successive favourable summers that would enhance tree recruitment and trigger treeline advance is unlikely (Camarero & Gutiérrez, 2004). Soil physical properties also play

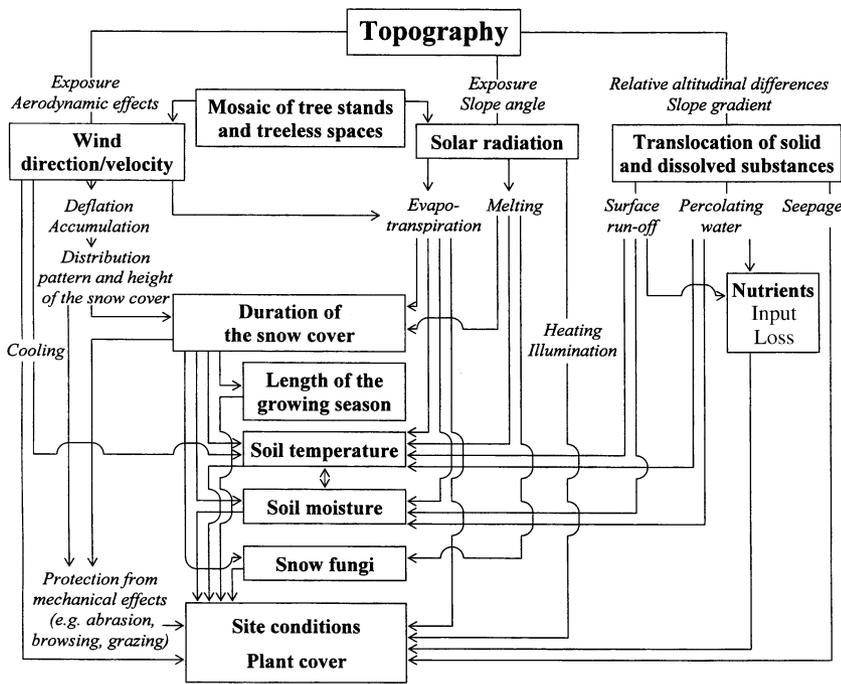


Figure 5 The influence of topography on site factors, site conditions and plant cover.

a role. Mineralization and nutrient supply depend on soil temperature, soil moisture and vegetation (quality and amount of litter), and are all related to the varying microtopography (Fig. 5). Thus, the direct influence of heat deficiency — or warming — on treeline sensitivity can hardly be isolated at the landscape and smaller scales. However, there are some good indicators in tree physiognomy and regeneration.

Indicators of climatic treeline sensitivity

Tree physiognomy. Climatic treelines, although caused mainly by heat deficiency, vary widely in physiognomy. Usually, trees close to the tree limit display climatically shaped growth forms. Tree physiognomy initiated by accelerated height growth, for example, of previously suppressed, low-growing trees (mat- or table-growth, 'Krummholz'; cf. Holtmeier, 1981) may be attributed mainly to the influence of changing environmental conditions as a result of a warming climate (see also Weisberg & Baker, 1995; Kupfer & Cairns, 1996; Scott *et al.*, 1997). Thus, in some cases, a reported 'treeline rise' is mainly the result of a phenotypical response of individual trees (now exceeding a minimum height considered to be the criterion for a 'tree') to more favourable climatic conditions (e.g. Kullman, 1979, 1986a,b, 2000; Lescop-Sinclair & Payette, 1995) rather than a real advance of tree growth to a higher elevation.

Nevertheless, this changing physiognomy does not necessarily reflect a long-term trend but rather the effect of a few favourable years allowing almost undisturbed growth above the extremely critical zone just above the snow surface. Dieback may occur due to deterioration of climate or extreme climatic events. Such climatically driven changes in tree physiognomy (Fig. 6) have repeatedly occurred in several northern and mountain treeline ecotones (e.g. Lavoie & Payette, 1992; Payette *et al.*, 1994; Scott

et al., 1997; Holtmeier, 2003). However, phenotypical change in trees may also be triggered by cessation of browsing as can often be observed on former alpine pastures and should not be mistaken for a climatic effect.

Seed-based regeneration. Generally, proneness of treeline ecotones to warming climate depends more on the success of regeneration (sexual, vegetative) at the present treeless sites within and beyond the ecotone than on morphological or physiological responses of mature trees (Holtmeier, 1993a, 1994b, 1995, 2003; Holtmeier *et al.*, 2003; Lescop-Sinclair & Payette, 1995; Weisberg & Baker, 1995; Hessel & Baker, 1997; Luckman & Kavanagh, 1998; Smith *et al.*, 2003). The production of fertile seeds depends mainly on sufficiently high ambient temperatures during a series of subsequent warm summers and is therefore very sensitive to climate warming. Reproduction from seeds has been and still is rare at the upper and northern tree limits, while often being abundant in open areas in the middle and lower parts of the mountain treeline ecotone. In the northern treeline ecotone, the northern limit of production of viable seeds is often far south of the northernmost tree stands (e.g. Holtmeier, 1974, 1994b, 1995, 2003; Nichols, 1975a,b; Elliott & Short, 1979; Black & Bliss, 1980; Elliot-Fisk, 1983; Larsen, 1989; Szeicz & MacDonald, 1995; Payette *et al.*, 2001). In mountains south of the northern (latitudinal) limit of production of viable seeds, supply of the treeline ecotone with fertile seeds is less critical because of the shorter distance from the seed sources at lower elevation. If climate warming continues, more regular sexual regeneration is likely beyond the present tree limit.

In contrast to mature trees several metres high, seedlings and young trees benefit from the relative favourableness of the microclimate, which is almost decoupled from the free atmosphere (e.g. Wegener, 1923; Wardle, 1974; Dahl, 1986; Holtmeier, 1987,

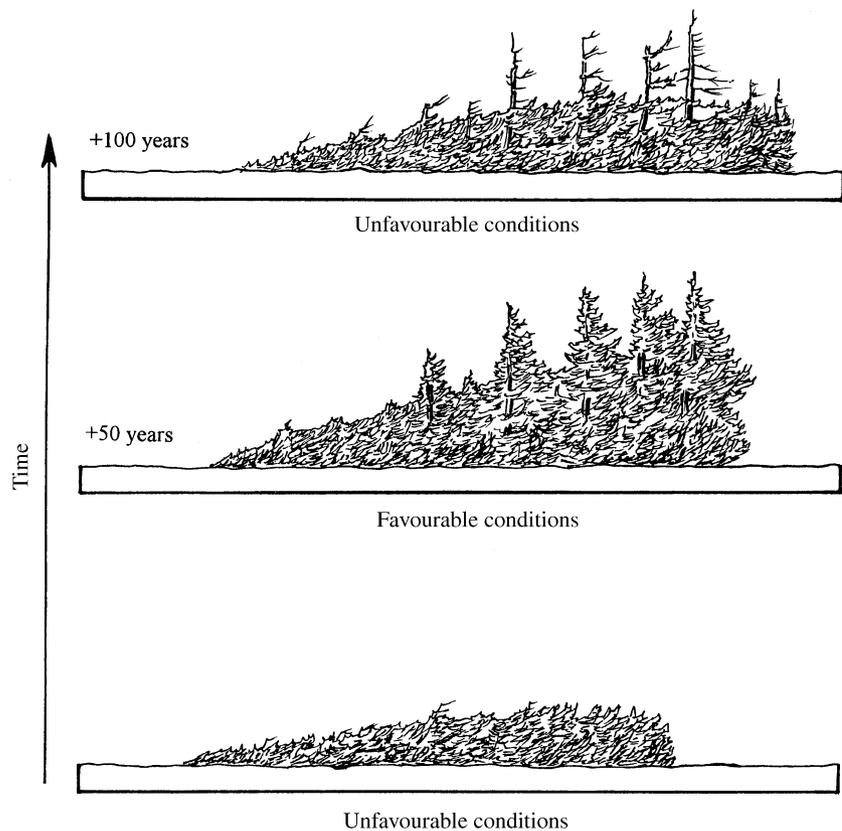


Figure 6 Change of tree physiognomy under changing climatic conditions (modified from Holtmeier, 2000).

2003; Wilson *et al.*, 1987; Grace, 1988, 1989; Grace *et al.*, 2002). However, in view of the many factors that can interrupt the reproductive processes (Fig. 7), seed-based regeneration may be considered an obstacle race, particularly at the northern treeline. Thus, regeneration success is probably a better indicator of the sensitivity of the treeline ecotone to environmental change than increasing growth of mature trees. One must be aware that increased temperature enhancing radial growth of mature trees may be in direct contrast to the successful establishment of seedlings if higher evaporation is not mitigated by higher precipitation and soil moisture (e.g. Daniels & Veblen, 2004; see also Fig. 8).

In most of our study areas, the extent of recent young growth has increased or is increasing in the lower and middle zones of the ecotone, whereas regeneration is still rare or almost does not occur at and beyond the actual limit of tree growth (Holtmeier, 1993a, 2003; Holtmeier *et al.*, 2003; see also Camarero & Gutiérrez, 2004). In many areas, increasing number of trees in the upper mountain birch treeline ecotone is mostly the result of the recovery of previously damaged birches that have viable basal sprouts developing from their still-living root stocks (e.g. Heikkinen & Kalliola, 1989; Kullman, 1991) and should not hastily be taken for a positive effect of climate warming on regeneration.

In other areas, young growth has become established at the former tree limit (e.g. Kullman, 2002). In the Scandinavian Mountains (Sweden), seedlings of mountain birch (*Betula pubescens* spp. *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) have recently become established 500–

700 m above their present tree limits (Kullman, 2004a,b). This increased number of seedlings apparently reflects improved changing climatic conditions. However, in the medium-term, this does not mean that forests will necessarily advance to greater elevation and more northern latitude (Holtmeier *et al.*, 2003), which would probably require much warmer subsequent summers than at present and would take centuries or even millennia (Skre *et al.*, 2002).

As emphasized by Smith *et al.* (2003), seedling establishment and abundance may involve considerable microsite facilitation [e.g. less sky and wind exposure, snow burial and protection of seedlings from frost drought, ice particle abrasion, etc. (Germino & Smith, 1999; 2000; Germino *et al.*, 2002; Smith *et al.*, 2003)], thus leading to an even greater seedling establishment (positive feedback). Establishment of seedlings may also be favoured by early snowmelt at the sun-exposed side of already existing tree islands (Holtmeier, 1986, 2003).

Trees, once established beyond the actual tree limit, can be very persistent (MacDonald *et al.*, 1993, 1998; Scott *et al.*, 1997) and may serve as seed sources and inoculation foci promoting infilling of the new range limits (Payette *et al.*, 1994, 2001; Kupfer & Cairns, 1996; MacDonald *et al.*, 1998; Burga & Perret, 2001). However, increasing numbers of trees will not necessarily have only positive effects on the treeline environment. There may be many negative feedbacks. For example, enhanced accumulation of wind-blown snow, particularly in open tree stands or on the leeward side of compact tree stands may curtail the growing season and increase the risk that the evergreen conifer seedlings

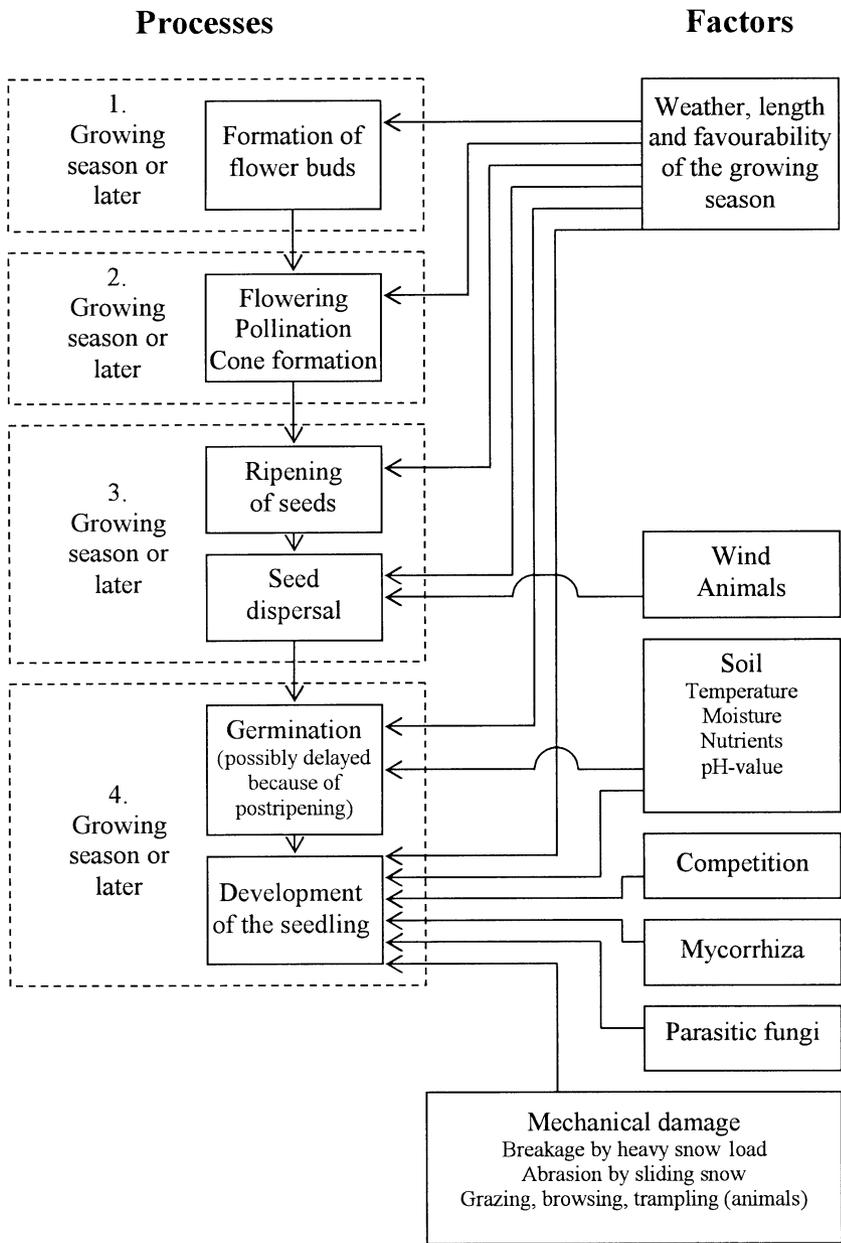


Figure 7 Factors and processes controlling seed-based regeneration at treeline (modified from Holtmeier, 1993a).

and young growth will fall victims to snow fungus infection (e.g. *Herpotrichia juniperi*, *Herpotrichia coulteri*, *Phacidium infestans*). Moreover, heavy snow loads may destroy seedlings (Holtmeier, 1993, 1996, 2003; Holtmeier & Broll, 1992).

In many regions, the tree limit has advanced less up to the present than might have been expected at the present degree of climatic warming (e.g. Wardle & Coleman, 1992; Butler *et al.*, 1994; Szeicz & MacDonald, 1995; Holmgren & Tjus, 1996; Crawford, 1997; Lloyd & Graumlich, 1997; MacDonald *et al.*, 1998; Peterson, 1998; Tasanen *et al.*, 1998; Cullen *et al.*, 2001; Camarero & Gutiérrez, 2004). Referring to their studies on spatial and temporal variabilities in the growth and climate response on treeline trees in Alaska, Lloyd and Fastie (2002) came to the conclusion that even at the coolest margins of the boreal forest, assumptions that rising temperatures have stimulated or will

continue to stimulate tree growth are unwarranted. Daniels and Veblen (2004) concluded from their treeline studies in northern Patagonia that an increase in temperature will not necessarily result in an upslope expansion of the *Nothofagus pumilio* forest.

Influence of climate character

At regional and smaller scales, sensitivity of the same treeline-relevant factors may vary in areas with different climatic characteristics.

In the strongly maritime mountains in western North America, for example, seed-based regeneration depends, as a rule, on the length of the snow-free season, whereas moisture conditions are the controlling factor in the drier regions (Fonda & Bliss, 1969; Kuramoto & Bliss, 1970; Woodward *et al.*, 1995; Holmgren

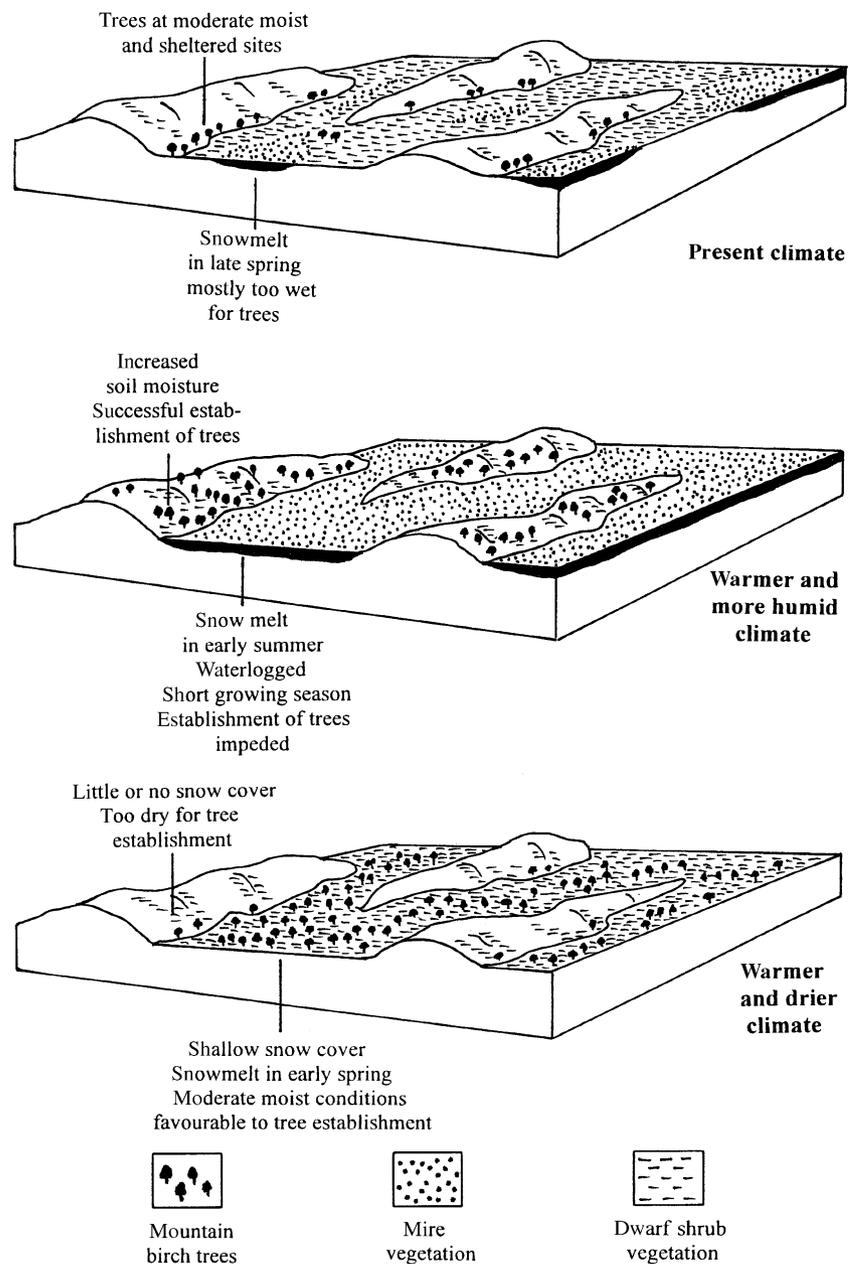


Figure 8 Scenario showing possible changes of a topographically controlled treeline pattern in northern Finnish Lapland under different climates.

& Tjus, 1996; Rochefort & Peterson, 1996; Peterson, 1998; Holtmeier, 2000, 2003; Holtmeier *et al.*, 2003). In the sub-alpine zone of Mt. Baker (North Cascades, Washington), which is characterized by a maritime, snow-rich climate, young growth that became established during the period 1925–45 was most successful on ridge crests, whereas late-lying snow and wetness impeded trees from invading valleys and other snow-rich depressions (Heikkinen, 1984). The same was observed in the treeline ecotone on Mt. Rainier in Washington (see also Lowery, 1972; Franklin & Dyrness, 1973).

In the Hudson Bay region or the West Siberian lowlands (maritime subarctic climate), warming is likely to enhance paludification, causing southward retreat of the northern limit of boreal forest (Crawford, 1978; Skre *et al.*, 2002; Crawford, 2005; Crawford *et al.*, 2003). In coastal regions of northern Fennoscandia,

for example, the effect of climate change on the length of the growing season has turned out to be different from inland regions (Hogda *et al.*, 2001). Spring starts earlier and autumn is delayed in coastal western Norway, which results in a prolonged growing season in this area. In the alpine zone, however, and in the boreal forest of northern inland Fennoscandia, spring is delayed, whereas the onset of autumn has not changed. Thus, the growing season has become shorter.

In more continental areas, climatic warming alone may exacerbate moisture stress, particularly on permeable substrates, if higher precipitation and snow pack do not compensate for increased evaporation. In the Rocky Mountain National Park (Colorado), regeneration of *Abies lasiocarpa* and *Picea engelmannii* increased considerably during the period 1940–70. This period was relatively warm and snow pack was higher than usual.

Meltwater probably alleviated moisture stress, which is often a limiting factor in this continental area of the Rocky Mountains (Hessl & Baker, 1997; Peterson, 1998). In the 1990s, after a drier period, we found 10- to 20-year-old young growth to be very rare in the Trail Ridge area (Rocky Mountain National Park; Holtmeier, 2003). Consequently, the present spatial structures of distribution and survival rate of regeneration in the treeline ecotone appear to be more sensitive to changes in moisture conditions than to warming (see also Daniels & Veblen, 2004).

The same holds true for our other continental study areas. On Beartooth Plateau (Montana), survival of whitebark pine seedlings that originated from seed caches of the Clark's nutcracker (*Nucifraga columbiana*) was much higher in shallow depressions with moderate snow cover than on wind-swept convex topography (Mellmann-Brown, 2002). In northern Finnish Lapland, cold spells that occurred during the growing seasons from the mid-1980s to early 1990s (Müller, 1999) — which might be expected to be fatal to seedlings and young growth — did not impede regeneration but rather improved moisture conditions at the rapidly draining sites (Holtmeier *et al.*, 2003). Such effects may completely override the influence of slightly increased regional temperature.

In the mountains of northern Finland (northern Utsjoki), shallow valleys and depressions appear to be more favourable to tree growth and seedling establishment than convex, wind-exposed topography, especially in areas where the substrate is permeable sandy glacial till. After the mountain-birch forest disappeared from convex topography due to cyclic mass outbreaks of the autumnal moth (*Epirrita autumnata*) and overgrazing by reindeer, the topsoil (the organic layer and the A-horizon) eroded from wind action (Fig. 4). Birch seedlings now have little chance of surviving at such sites, but occur at relatively high density at wind-protected, snow-rich, nutrient-rich and moist shallow valleys and similar concavities. We found up to 25 seedlings, aged 5 years or less, per square metre, locally even more. Because young growth older than 5 to 8 years (at the end of the 1990s) was still very rare, we speculated that the relatively great number of younger seedlings indicates environmental change or, at least, a positive fluctuation (Holtmeier *et al.*, 2003).

In north-western Finland (Kilpisjärvi area), birch seedling density is also comparatively high in soaked, snow-rich sites, such as shallow valleys and similar depressions on mountain slopes, whereas seedlings are rare on wind-swept and dry convex topography (Holtmeier *et al.*, 2003). Mountain birch stands that had become locally established in snow-rich wet sites above the pine forest in the Swedish Scandes during the 'warm period' (boreal-subboreal, 9000–2500 BP; Kullman, 1983; Aas & Faarlund, 2001) probably reflect the same rule.

The question arises therefore as to how recent tree regeneration in wet snow-rich sites will respond to increasing snow pack. With greater snowfall, regeneration might be impeded because of a shorter snow-free season. Under a more continental climate, such as in Finnish Lapland, sites that are too dry at present might become more favourable to tree establishment (Fig. 8). Preliminary scenarios predict a 3% increase in winter precipitation per decade and none in summer for Finnish Lapland (Saelthun,

1995). Therefore, birch density might increase, provided that no other factors (e.g. increasing evaporation in summer, extreme climatic events, reindeer grazing) adversely affect invading birches.

Influence of local topographic structures on treeline sensitivity

Climatic treelines can be differentiated by their topographical structures within and beyond the present treeline ecotone. Microtopographical structures on steep mountain slopes are different from those on gentle slopes or almost horizontal surfaces.

Steep slopes. Steep mountain slopes (valley sides) in the European Alps, for example, often exhibit rib-and-groove topography caused by postglacial erosion. On ribs and similar convex topography, trees and young growth may climb to their climatic limit. Approaching the climatic limit, tree stature decreases and tree individuals are increasingly deformed by adverse climatic effects. In the grooves, snowslides and avalanches usually prevent the forest from reaching its climatic limit. The zone most sensitive to changing climate is at the upper edge of the ecotone on the ridges, where warming may enhance growth rates and sexual regeneration. Also, the trees might develop less stunted or even undisturbed growth forms. This treeline pattern, rib-and-groove topography, shows little sensitivity to climate change. This also holds true for the steep trough walls in U-shaped mountain valleys. The situation is different, however, on the more gently sloping and usually less intensely sculptured trough shoulders from which the forest was almost completely removed by humans.

Gentle slopes. On gentle slopes, regular rib-and-groove topography is usually missing. Avalanches do not occur, and orographic influences such as rocky outcrops or rock debris are locally confined. The mountain forest may advance to its upper climatic limit in almost a closed front. In this case, the treeline ecotone may be relatively narrow. Close to the upper limit of tree growth the forest usually disintegrates into tree groups and solitary trees mainly because of the effects of convex and concave microtopography on site and growing conditions. Often, the uppermost tree groups became established during periods relatively favourable to seedling survival and tree growth, and persisted mainly by layering (Fig. 6). With warmer conditions, they may become an important seed source. However, seedlings are still very rare at and beyond the tree limit. The open patches appear to be most sensitive to warming and might be invaded by tree growth in the future. However, large snow masses regularly accumulating in these glades may prevent successful regeneration, particularly in snow-rich years. Thus, young growth might more easily invade the treeless zone above if sufficiently resistant to climatic injuries.

Level terrain. On almost level terrain, such as old up-lifted land surfaces, northern peneplains and lowlands, the treeline ecotone is usually wide (hundreds or even thousands of metres) compared to the ecotone on mountain slopes. Microtopography caused a more or less varying mosaic of dense tree clumps and

open tree stands alternating with subalpine/alpine or tundra vegetation. The patchiness is caused not only by microtopography but also — particularly in case of smooth microtopography — by the influence of the more or less dense tree and 'Krummholz' stands themselves on wind-driven snow and its effects on other site factors (cf. Fig. 5; Holtmeier, 1993a, 2003; Broll & Holtmeier, 1994). Sensitivity of the existing (often relictual) treeline structures to a warming climate and proneness to change will increase provided that there is a sufficient supply of fertile seeds and if warming compensates for extreme site conditions on wind-swept convex topography with little snow or no snow in the winter and in extremely snow-rich and poorly drained concave sites. This would allow sustainable establishment of tree growth at presently treeless topography. Forest will not generally advance in a closed front but will follow sites that became more favourable to tree growth under the changed climatic conditions (Holtmeier, 1990, 1995; Burga & Perret, 2001).

On the only gently sculptured northern peneplains and lowlands, the situation is a little different from that on old up-lifted land surfaces in mountainous regions because comparatively wider areas are characterized by poor drainage conditions. In maritime regions, warming would increase paludification (due to increased precipitation and cloudiness) and may cause a retreat of the forest and tree groves to better drained topography (e.g. low hills, ridge moraines). Regionally, forests may recede for tens or even hundreds of kilometres to a more southern position rather than advancing north.

CONCLUSIONS

In the long term, continued global warming will facilitate treeline advance to greater altitude and latitudes. However, the sensitivity of treelines to environmental change, and in particular, to climate warming, varies with local and regional topographical conditions and thus differs as to its extent, intensity and the process of change.

At the landscape and local scales, the effects of topography on site conditions often override the effects of global warming. They are not very likely to change substantially in the foreseeable future.

With favourable site conditions, regional warming may result in better growth of trees and production of viable seeds. However, higher production of fertile seeds does not automatically result in increasing establishment and survival of seedlings in presently treeless sites within the treeline ecotone and beyond the tree limit because other factors may have opposing effects. In this respect, the interannual variability of climate plays an important role.

The effects of the same site factor on tree establishment may be different in continental and maritime climates. Therefore, careful local and regional studies considering such effects are needed to assess more accurately the sensitivity of the treeline to present and future warming.

Spontaneous advance of young growth into treeless areas within the treeline ecotone and even beyond the present tree limit, as well as increasing height growth of suppressed trees and more 'normally' developing tree crowns, may prove to be the best

indicators of treeline sensitivity to environmental change at the landscape and local scales, in the short to medium-term perspective, rather than the growth of mature trees. Research on the factors controlling spatial and temporal patterns of establishment and survival of seedlings and young growth should be intensified.

Orographically controlled treelines are relatively insensitive to changing climate. They will not advance to the potential climatic tree limit (greater altitude) as long as mass wasting, debris slides and avalanches occur.

Great sensitivity and more rapid change can be expected in anthropogenic treelines after the cessation of human activity. However, establishment of trees above the anthropogenic forest limit is more impeded by extreme microclimates resulting from the removal of the forests than is generally recognized. In many locations, the amplitude and magnitude of recent warming might not be sufficient to compensate for what is left from a detrimental arboreal history. Therefore, the high sensitivity of treelines to climate warming alleged from many high mountain and also subarctic regions should be considered *cum grano salis*.

As to the assessment of the sensitivity of the altitudinal and northern treelines to environmental change and in view of the great physiognomic and ecological variety and heterogeneity of the altitudinal and northern treelines, regional differentiation (landscape and smaller scales) is needed if a global view is to be obtained. This, however, can be achieved only by filling the gaps in the present knowledge on both the altitudinal and northern treelines by careful investigations at the regional and smaller scales. Future research should focus on the relative importance of the factors involved in shaping treeline physiognomy, pattern, and dynamics. In the final analysis, the direct influence of temperature on tree growth (mature trees) may not necessarily be the decisive factor.

The search for treelines suitable for monitoring for the first effects of present climate change at the regional, landscape or local scales, should focus on treelines undisturbed by orographic effects and human impact. Satellite imagery and other remote sensing techniques can facilitate the identification of those treelines that are most appropriate for this type of field research, even in remote areas.

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