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Treeline advance
– driving processes and adverse factors

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Abstract

The general trend of climatically-driven treeline advance is modified by regional, local and temporal variations. Treelines will not advance in a closed front parallel to the shift of any isotherm to higher elevations and more northern latitudes. The effects of varying topography on site conditions and the after-effects of historical disturbances by natural and anthropogenic factors may override the effects of slightly higher average temperatures. Moreover, the varying treeline-forming species respond in different ways to a changing climate. Forest advance upwards and northwards primarily depends on successful regeneration and survival of young growth rather than on increasing growth rates of mature trees. Every assessment of treeline response to future climate change must consider the effects of local site conditions and feedbacks of increasing tree population in modulating the climatically-driven change. Treeline-shift will influence regional and local climates, pedogenesis, plant communities, animal populations and biodiversity as well as having a considerable effect on economic changes in primary production. A better understanding of the functional relationships between the many treeline-relevant factors and treeline dynamics can be achieved only by extensive research at different scales within different climatic regions supported by as many as possible experimental studies in the field together with laboratory and remote sensing techniques.

Keywords
Treeline pattern, treeline history, treeline dynamics, climate change, regeneration

1 Introduction

After the major mid-Holocene treeline retreat (ca. 4000 - 5000 BP) it has been necessary to wait until the end of the "Little Ice Age" in the late 1800s to witness the initiation of migration of plants and shifts of climatic treeline to greater elevations and higher latitudes. This review concentrates first of all on the changes that have been observed in the altitudinal and polar treeline ecotones of the northern hemisphere during the favourable climatic period from the 1920s to the 1940s (1950s) and during the last three decades (Holtmeier 2003, there further references). Comparatively little information is available on treeline response to present climate changes in the southern hemisphere and in the tropics (Rundel et al. 1994; Villalba et al. 1997; Wardle & Coleman 1992; Cuevas 2000, 2002; Biondi 2001; Cullen et al. 2001; Bader 2007).

From a global view point, the increase of thermal deficiency with increasing altitude and latitude is the ultimate cause affecting tree physiological processes. From this it follows that regeneration and survival are also affected both directly and indirectly. Various other modifying factors such as wind, or late-lying winter snow pack, energy loss through snow melt, and evaporation also have to be considered. The limiting role of heat-deficiency is clearly reflected in the gradual decline of the treeline from its maximum altitudinal position in the subtropics towards the poles, and in tree stature decreasing towards the tree-limit. There are nevertheless exceptions as in some semi-arid or arid inland mountain areas and several oceanic subtropical islands low precipitation and limited plant available water during the growing season are likely to be controlling position and local pattern of treeline (e.g., Troll 1973; Horvat et al. 1974; Henning 1974; Wardle 1974; Höllermann 1978; Leuschner & Schulte 1991; Leuschner 1996; Brandes 2006). This global pattern is underlain by more or less great regional and local variations (cf. Arno 1984; Holtmeier 2003).

Altitudinal and polar treelines are conspicuous landscape boundaries. They usually occur as more or less wide ecotones characterized by specific ecological conditions that differ from those of the closed mountain and northern (subarctic) forests and alpine or northern tundra (Holtmeier 2003). Thus, treeline advance to higher elevation and a more northern position will bring about fundamental landscape changes in mountains and subarctic regions.

2 Present change at treeline

In the northern hemisphere, the climatically-driven advance of altitudinal and polar treelines is ubiquitous. The general trend, however, is being modified by more or less great regional, local and temporal variation as a result of the regionally varying magnitude of climate change and the role of the historical legacy of the landscape (climate, vegetation, soils, human use, etc.; e.g., Kearney & Luckman 1983; Kullman, 2000, 2005a, 2005c; Holtmeier 1985, 1993, 2003; Luckman & Kavanagh 1998; Lloyd et al. 2003; Lloyd & Fastie 2002; Dalen & Hofgaard 2005; Lloyd 2005; Gamache & Payette 2005). This is demonstrated in the following examples.

At the treeline along the east coast of the Hudson Bay, for example, recent warming has not been strong enough to allow establishment of trees until the 1990s (Lescop-Sinclair & Payette 1995). At the northern treeline in the Ennadai-Lake area (central Canada), no young growth became established until the late 1970s (Elliott 1979) while intense regeneration simultaneously

occurred at the treeline in Labrador (Elliott & Short 1979; Elliott-Fisk 1983). In the Churchill area (Hudson Bay, Manitoba), the tree population increased within the treeline ecotone while young growth did not become established at treeline until the end of the 1980s (Scott et al. 1987). In northern Québec, no young growth has occurred until recently. Probably, the amplitude and magnitude of recent warming has not been large enough to compensate at such extreme locations for what is left of the negative after-effects of the "Little Ice Age" (Payette et al. 1989; Lescop-Sinclair & Payette 1995). Kullman (1990) reported a similar situation at a treeline on the Swedish Scandes, where since the early 1970s no regeneration had occurred until the late 1980s.

Figure 1: Organic layer and upper mineral top soil have been eroded by wind on this exposed site (327 m) on Koahppeloaivi in northernmost Finnish Lapland. Lack of moisture and nutrients prevent birch from invading this formerly forested site. Photograph taken by F.-K. Holtmeier, 21 August 2004

In some localities of the Swedish Scandes, great numbers of fast-growing 10-15 years old saplings of mountain birch, spruce and pine occur 400-500 m or even up to 700 m above the current tree limits (Kullman 2003, 2004, 2005a, 2005c). In the Handölan Valley (southern Swedish Scandes) Scots pine (*Pinus sylvestris*) population increased overall by 50% during a 32-year monitoring period

(1973-2005) despite having declined during the first decade. The consistent expansion that has taken place since the late 1980s more than compensates for the earlier decline. It appears that the exceptionally warm summers since 1997 and low mortality rates due to milder winters have been responsible for the improved establishment of pine seedlings (Kullman 2007). In other places, height growth of climatically-stunted trees in wind-exposed sites with little or even no snow in winter is still impeded, despite the generally warmer climate (cf. Holtmeier 2003, 2005a, 2005b; Kullman 2005b).

On the mountains in Finnish Lapland, where a general trend of treeline advance is obvious (e.g., Juntunen et al. 2002), regeneration and seedling establishment vary considerably among the localities. In some areas of northernmost Finnish Lapland, for example, Holocene forest decline was locally followed by severe soil erosion (Fig. 1). Wind-eroded soils poor in nutrients and characterized by low water-holding capacity prevent mountain birch from resettling formerly forested sites within the treeline ecotone and beyond the present tree limit. (e.g., Holtmeier et al. 2003; Holtmeier et al. 2004; Kullman 2005c; Anschlag 2006; Broll et al. submitted).

This contrasts with the general "rule" that bare mineral soil surfaces provide favourable seed beds for wind-mediated tree seeds (e.g., larch, birch: e.g., Holtmeier 1967a, 1967b; Kinnaird 1974; Löffler et al. 2004), mainly because competition with dwarf shrubs or grass vegetation is absent or reduced (see also Kallio & Lehtonen 1973; Hobbie & Chapin III 1998). Overgrazing by reindeer, however, appears to be the most harmful factor for birch seedlings.

On the fells in western central Finnish Lapland, Scots pine seedlings (*Pinus sylvestris*) became established at great numbers in the treeline ecotone during the favourable period from the 1920s to the 1940s (cf. Hus-

tich 1937, 1942, 1958; Blüthgen 1942; Holt-meier 1974; Holtmeier et al. 1996; Holtmeier et al. 2003), while comparatively few pines occurred in and above the birch-treeline ecotone on the fells in the northernmost part of Finland during the same period of time. It is probable that climatic conditions were less favourable than on the more southern fells (Autio & Colpaert 2005). Thus, current pine advance into the birch-treeline ecotone and alpine tundra on the northern fells (Fig. 2) may be attributed to recent environmental change, which also initiated intensive regeneration on Pallastunturi (south-western Finnish Lapland). In this area, the number of seedlings has increased again since the 1970s, particularly since the mid-1980s until the end of the 20th century (Holtmeier et al. 1996; Tasanen et al. 1998; Holtmeier et al. 2003; Holtmeier 2005b).

In Norway, regional differences in treeline response to climate warming are apparent. Stable or advancing treelines are common in the southernmost and probably in the middle regions while treeline is declining in the north (Dalen & Hofgaard 2005).

In New Zealand, recent, continuous establishment of seedlings in the *Nothofagus menziesii* treeline forests has not occurred nor has there been any upslope treeline movement. Recruitment continues to be as episodic as ever. Very likely, the absence of the natural disturbances that would create canopy openings is the main factor preventing seedling establishment (Cullen et al. 2001). In northern Patagonia, *Nothofagus pumilio* has not successfully regenerated at the treeline although the temperature has risen since 1970 (Daniels 2000). Regeneration failed probably because of moisture deficiency. This means that tree establishment above the present forest would only be possible if warming coincided with canopy disturbance (New Zealand) or favourable moisture conditions (Patagonia).

In the Spanish Pyrenees, warm springs and wet summers enhanced pine regeneration (*Pinus uncinata*) within the treeline ecotone between 1955 and 1975. However, the tree limit did not advance (Camarero & Gutiérrez 2000).

Regional, local and temporal variations may also be a consequence of the different response of tree species to changing climate. On Beartooth Plateau (Montana/Wyoming), for example, seedlings of whitebark pine (*Pinus albicaulis*) have originated from seed caches of the Clark´s nutcracker (*Nucifraga columbiana*) during the last decade. By contrast, seedlings of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are almost absent (Mellmann-Brown 2002, 2005).

Figure 2: Young Scots pine (*Pinus sylvestris*) which became established at an altitude of 225 m in the birch treeline ecotone on Staloskaidi in northernmost Finnish Lapland during the late 1980s. The pine, which is still protected from winter-injury by the snow cover and by the dwarfshrubs, shows undisturbed vertical growth. Since 1998 height growth has accelerated. Photograph taken by F.-K. Holtmeier, 8. August 1999.

In the Colorado Front Range, Engelmann spruce is being more successful in invading treeless terrain at high elevation than is subalpine fir (Holtmeier 1999).

On Pallastunturi (see above), spruce seedlings (*Picea abies*) prevail and pine seedlings (*Pinus sylvestris*) are common. The number of birch seedlings (*Betula pubescens* ssp. *czerepanovii*), however, abruptly declines within a few meters distance from the seed trees growing in the upper orchard-like birch stands (Tab. 1; Holtmeier et al. 2003).

Probably, the after-effects of landscape and site history are the most important agents shaping the present treeline. Primary and secondary succession (after disturbances), competition, natural and man-caused forest fires, heavy wind storms, extremely snow-rich winters or winters almost without snow, droughts, mass outbreaks of leaf-eating insects, and other extreme events often have a lasting impact. In the central Norwegian mountains (Møre and Romsdal County), for example, present plant species composition and distribution pattern of the plant communities in the treeline ecotone and lower Alpine is strongly related to environmental conditions "inherited" from the former forest, which has retreated steadily during the Holocene (Hofgaard & Wilmann 2002).

The decline of the natural climatic treeline in the European Alps after the postglacial optimum was considerably accelerated by human impact such as pastoral use, mining, saltworks, charcoal production, etc., particularly during the Middle Ages (Fig. 3). Modern changes in economic structure have resulted in invasion of abandoned alpine pastures by trees. However, seedlings and young growth are being more affected by injurious climatic and biotic (snow fungi infection) influences than might be expected due to the anthropogenically caused low position of the present forest limit (cf. Fig. 3; see also Holtmeier 1967a, 1967b, 1974, 2003; Stützer 2000).

Moreover, gradually closing plant cover influences invading tree species differently. European larch (*Larix decidua*), a typical pioneer species on unvegetated or exposed mineral soils, is less successful than zoochorous Swiss stone pine (*Pinus cembra*) in resettling abandoned alpine pastures once a dense grass and dwarfshrub cover has developed (see also Holtmeier 1967a, 1967b, 1995b: Müterthies 2002). Grass cover also prevents prostrate mountain pine (*Pinus mugo*) from invading abandoned subalpine pastures in some areas of the northern limestone Alps. On the other hand, mountain pine is likely to invade rapidly alpine grassland at and above the present tree limit where competition with other vegetation is reduced (Dullinger et al. 2003, 2004). Competition with dense dwarfshrub vegetation seems to be impeding mountain birch establishment also at the treeline in Vågå upland (southern central Norway; Löffler et al. 2004).

"Relic treelines" that became established at relatively high altitude under a warmer than the present climate, as on many ranges of the Rocky Mountains (Ives 1973, 1978; Ives

Table 1: Percentage of tree seedlings in altitudinal transects of Pallastunturi *)

| Tree species [%] | Palkaskero Transect 1 n = 52 | Palkaskero Transect 2 n = 84 | Palkaskero Transect 3 n = 83 | ------Pyhäkero transect------- | |
				up to 550 m n = 37	550 m – 745 m n = 15
Norway spruce	77	70	70	30	67
Scots pine	17	25	21	20	27
Mountain birch	6	5	9	50	6

*) Data from Holtmeier et al. 2003

**Historical
human impact**

• Pastoral use
• Burning
• Mining
• Salt works
• Charcoal production
• Timber harvesting
• Oversized game
  population

Degradation and
over-aging of
high-elevation forests

Retreat of forest and
tree limits

**After-effects
retarding tree invasion above the
anthropogenic forest limit after
decrease or cease of human use**

Extreme microclimates
    on wind-exposed topography
        • Abrasion
        • Frost drought
        • Frost
        • Photo inhibition
    on snow-rich topography
        • Short growing season
        • Snow fungus infection
        • Delayed root growth
Snow creep
Snow slides
Avalanches

Competition with dwarfshrub and grass
vegetation

Impoverished mycorrhizal flora

Soil erosion

Herbivory

Figure 3: Historical human impact and effects on treeline dynamics, Central Alps.

& Hansen-Bristow 1983; Holtmeier 1985, 2003), for example, were characterized by increasing tree population within the treeline ecotone (Fig. 4) rather than by the establishment of seedlings above the upper limit of the climatically stunted trees ("krummholz"). A similar situation has been reported from the subarctic altitudinal treeline of northwestern Canada (Szeicz & MacDonald 1995). More recently, however, and locally increasing numbers of tree seedlings can also be found beyond the tree limit (Fig. 5).

In many treeline ecotones, accelerated height growth of hitherto suppressed, low-growing trees (e.g., mat- or table-growth) rather than recent establishment of young growth beyond the existing tree limit indicates environmental change. Many of these formerly suppressed trees now exceed the minimum height considered to be a criterion for a "tree" (e.g., Kullman 1987, 2000, 2002, 2005a, 2005b, 2005d; Lavoie & Payette 1992; Lescop-Sinclair & Payette 1995; Kjällgren & Kullman 1998; Tasanen et al. 1998; Gamache & Payette 2004, 2005; Vallé & Payette 2004). In other places, extreme events such as drought or severe frosts during the growing season have locally caused setbacks to tree development (Fig. 6).

In many mountain regions the treeline has not advanced or advances less than expected during recent decades in relation to the extent of climatic warming (e.g. Holtmeier 2003; Wardle & Coleman 1992; Lloyd & Graumlich 1997; MacDonald et al. 1998; Peterson 1998; Tasanen et al. 1998; Cullen et

Figure 4: Seedlings of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) invading a swale (3373m) within the treeline ecotone of the Blue Lake Valley, Colorado Front Range. The swale was treeless in the early 1970s. Photograph taken by J. B. Benedict, 27 July 2006.

Figure 5: Young Engelmann spruce (*Picea engelmannii*) invading the alpine tundra on a south-exposed slope on Ida Ridge (Rocky Mountain National Park, Colorado). The highest new colonist is at an altitude of 3612 m. Photograph taken by J. B. Benedict 28, July 2006.

al. 2001; Holtmeier et al. 2003; Holtmeier & Broll 2005; Mazeda 2005). Lack of current change, however, may be an after-effect of a fast local response in the past (e.g., Butler et al. 1998; Malanson 2001).

Insufficient carbon gain has long been considered to be the factor setting an absolute limit to high-elevation tree growth (see Tranquillini 1979 and Holtmeier 2003 for further references). Thus, increasing CO_2 is expected to trigger altitudinal advance of treeline (e.g., Walsh et al. 1992). However, there has been no evidence of significant correlation of enriched CO_2 and tree growth at treeline, thus far. Other factors seem to override the effects of increased CO_2. For example, increased diameter growth that has occurred in bristlecone pines (*Pinus longaeva*) in the treeline ecotone on the White Mountains (California) and limber pine (*Pinus flexilis*) on Mt. Washington (Nevada) (LaMarche & Mooney 1972; LaMarche et al. 1984) since the middle of the 19th century must be ascribed to increased precipitation rather than

to enriched CO_2 and/or higher temperatures (Stockton 1984). Diameter growth of subalpine trees in the Cascades remained unaffected by increased CO_2 and declined since the favourable 1940s, following the regional trend of temperature (Graumlich & Brubaker 1986; Graumlich et al. 1989). In the southern Sierra Nevada, last year's precipitation and current summer temperature have been completely overriding the effects of CO_2-fertilization (Graumlich 1991). This supports the hypothesis of Körner (2003) that continuing increase in atmospheric CO_2 is unlikely to enhance tree growth and treeline advance on a global scale. The abundance of such conflicting research results ensures that discussion on this is likely to continue (e.g., Smith et al. 2003; Johnson et al. 2004).

Altogether, the present conditions within the treeline ecotones can be explained only in view of the historical disturbances by natural and anthropogenic factors (cf. Fig. 3; see also Fig. 14). The current climate often has

Figure 6: Severe winter injury to a clonal conifer group (*Picea engelmannii* and *Abies lasiocarpa*) near Devil`s Thumb at an altitude of 3420 m (Colorado Front Range). The damage which is reflected in the discoloured, reddish needles and shoots (see arrow) was very likely caused or predetermined by an extreme frost in September 1995. The basal part of the trees, which is protected by the winter snow pack, was not affected. The damage will have a lasting effect on future growth of these trees. Photograph taken by J. B. Benedict, 6 August 1996.

only a modulating effect. Past natural and anthropogenic disturbances have produced a spatial-temporal mosaic of patches at different successional stages. In many areas, they are the factors responsible for resilience of present treeless areas within the present treeline ecotone to invasion by trees in face of a warming climate.

3   Expected change at treeline

The relationship of the altitudinal or latitudinal positions of the treeline to the future thermal conditions is currently of great interest, both from a global viewpoint as well as for regional and local concerns. However, predicting the future treeline is problematic and often imponderable. Thus,

projecting the present relation of treeline and a certain isotherm considered to be the tree-growth limiting factor into a warmer future may be misleading as in many places the present position of treeline is not in balance with the current climate. This holds particularly true for the altitudinal treeline in the high mountains of Eurasia, many of them being settled throughout history (Holtmeier 2003, further references therein). Another reason is the inertia of trees that became established some hundred years ago (Fig. 7; see also Fig. 6) under different climatic conditions from those that prevail at present climate (e.g., Larsen 1965; LaMarche & Mooney 1967; LaMarche 1969; Tolmachev 1970; LaMarche & Mooney 1972; Ives 1973; Krebs 1973; LaMarche 1973; Nichols 1976; LaMarche 1977; Ives 1978; Elliott 1979; Payette & Gagnon 1979; Larsen 1980; Hansen-Bristow 1981; Légère & Payette 1981; Ives & Hansen-Bristow 1983; Holtmeier 1985, 1986; Larsen 1989; Brunstein & Yamaguchi 1992; Payette & Morneau 1993; Kullman 2000). Moreover, we are used to basing "predictions" of treeline on our knowledge of past and current treeline dynamics which brings in additional problems. We have to be aware that we do not really know whether the present interrelationships of temperature and the many other tree-growth influencing factors and their relative effectiveness will be the same in a warmer climate (see also Giorgi & Hewitson 2001; Holtmeier 2003; Holtmeier & Broll 2005). Furthermore, it is still an open question which effects will result from a delayed response of treeline to a rapid climatic change. Thus, the following "predictions" are speculative.

The linkages between tree-cover and permafrost, for example, will be different. In subarctic lowlands such as the Hudson Bay area and western Siberia increasing paludification, as a consequence of the warming climate and melting permafrost, is likely to cause a southward retreat of the boreal forest (e.g., Crawford 1978, 2005; Crawford et al. 2003). In high mountains such as the

Figure 7: Bristlecone pine (*Pinus aristata*) on Kingston Peak (Colorado Front Range) at an altitude of about 3360 m. This extremely wind-shaped pine became established more than 1000 years ago. Its physiognomy has not changed very much in course of time. Seedlings did not become established at this site. Photograph taken by F.-K. Holtmeier, 2 August 1987.

Alps, melting of local permafrost at high elevations will result in destabilization of steep mountain slopes, thus increasing erosion of potential forest sites (Fig. 8; Burga & Perret 2001; see also Harris 2005). At more wet-snow conditions (usually in spring and in maritime regions) snow fungi infection might increase and reduce survival of seedlings and young growth of evergreen conifers (Holtmeier 2005a, 2005b), whereas in a warmer and drier climate, earlier snow melt will reduce the risk of snow fungus infections.

Nevertheless, earlier snow melt will expose seedling and saplings to late frost and drought. The effects of soil permeability, for example, may also be different in dry regions compared to humid regions (Holtmeier & Broll 2005). In dry climates, high permeability may result in moisture stress to seedlings and saplings. In humid climates, high permeability is likely to improve aeration of the rooting zone. Moreover, factors and processes at one scale may not be as important at another scale (Turner 1989; Holtmeier & Broll 2005). Insufficient soil moisture and nutrient supply, for example, which may affect seedling establishment at the local scale will be less important in a global view of the factors controlling treeline dynamics.

Because the effects of varying topography on site conditions may locally override the effects of slightly higher average temperatures treelines will usually not advance in a closed front parallel to the shift of any isotherm. Exposure to solar radiation, wind velocities and directions, as well as snow distribution pattern and resultant effects (e.g. length of the growing season, snow fungus infection of evergreen conifers, mechanical

damage to trees) will be playing an important role in this respect (e.g., Holtmeier 2003, 2005a; Kullman 2005b). Likewise, soils, soil temperature, soil moisture and mineralization will all play a role. By their physiological and mechanical effects permanent strong winds may suppress tree growth or produce dwarfed growth forms that may assume upright growth if climate will become more favourable (Fig. 9). A deteriorating climate may cause dieback again (cf. Fig. 6).

Moreover, treeline response to changing climate will vary with tree species and type of treeline (e.g., Luckman & Kavanagh 1998; Holtmeier 2003; Holtmeier & Broll 2005). Treeline type depends on topography, tree species represented, and on history of landscape, climate and vegetation. In a warmer future, Engelmann spruce or subalpine fir (Rocky Mountains), for example, that have

reproduced mainly by layering in the past are likely to regenerate preferentially by seedlings. This may have a sustainable effect on treeline dynamics.

In the long-term perspective, local topography is the only relatively constant factor in the treeline environment that will not be affected by climate change. In mountainous regions, topography may be highly variable over relatively short distances. Topography on steep mountain slopes differs from topography of a glacially moulded valley, a gently rolling uplifted land surface or a smoothly sculptured subarctic peneplain (Holtmeier 2003; Holtmeier & Broll 2005). Treelines on a rolling peneplain (e.g., Gamache & Payette 2004, 2005) will respond in a different way to a warming climate than will treelines on rugged mountain topography. In many steep-sided high mountain val-
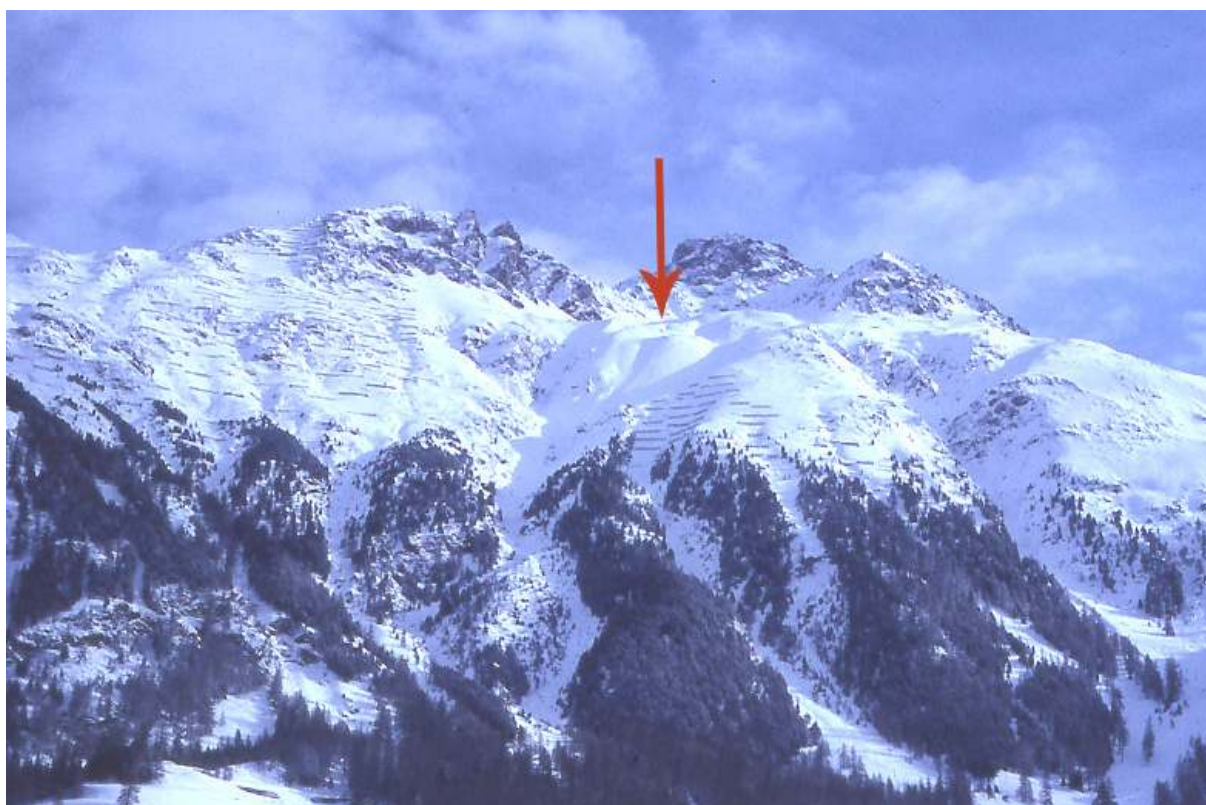

Figure 8: View of the mountain slopes above Pontresina village (Upper Engadine, Switzerland). The arrow indicates an area of melting permafrost in a glacial cirque (2800 m). Permafrost melt is likely to trigger a disastrous outburst of block-debris and mud that would destroy the present forests and impede climatically-driven forest advance for a long time. Photograph taken by F.-K. Holtmeier, February 1969.

Figure 9: Wind-shaped limber pines (*Pinus flexilis* on a wind-swept saddle (3450 m) in the treeline ecotone on Wheeler Peak (Nevada). Improving climatic conditions have allowed some terminal leaders to develop into erect stems. Photograph taken by F.-K. Holtmeier, 30 July 1994.

leys, high avalanche activity (cf. Fig. 8), mass wasting, instable slope debris and fragmented or missing soil cover prevent forest from reaching its possible thermal altitudinal limit (Fig. 10) while those factors do not occur on flat or gently sloping topography.

Moreover, treelines will respond to rising temperatures mainly with gradual infilling of the gaps between the existing trees and tree groups and, to a lesser extend, with the establishment of trees in places above the present tree limit (cf. Figs. 4 and 5). Even under continued favourable climatic conditions the altitudinal and polar shift of the treeline may lag behind climate change by decades or even centuries (Holtmeier 1985, 1986, 2003; Davis 1986; Woodward 1998; Noble 1993; Hofgaard & Wilmann 2002; Lloyd 2005). Inter-annual and inter-decadal climate variability causing abrupt and reversible effects have played and will play an important role as may

be hypothesized in respect of recent treeline history (e.g., Bugmann & Pfister 2000; Müterthies 2002; Millar et al. 2004). Treelines influenced by pastoral use for centuries will respond to a warming climate in a different way than undisturbed treelines. Abandoned pasture areas above the man-caused forest limit will continue to be rapidly invaded by trees. However, establishment and survival of seedlings may be hampered more by negative effects of microclimates resulting from the historical removal of the high-elevation forests than should be expected at the low level of the present forest limit (cf. Fig 3). Severe microclimates are more likely than global warming to control treeline dynamics at a local level, at least in the next future. In the long-term, however, increasing tree populations may have a mitigating effect.

Forest advance to higher elevations and more northern latitudes does not and will in general not depend on increasing growth rates of mature trees and change in growth form from "krummholz" to erect stems (cf. Fig. 9) but on successful regeneration and survival of young growth (Holtmeier 1993; Smith et al. 2003). The survival rate of seedlings has been generally low in the treeline environment during the first years after germination (e.g., Cui & Smith 1991; Mellmann-Brown 2002). However, this may change in a warmer climate. Generally, the regeneration process is positively correlated to favourable thermal conditions of several sequential years (Fig. 11). Warmer summers are likely to favour production of viable seeds, seedling establishment and thereby tree recruitment in the present treeline ecotone provided that other factors do not interfere. Such factors will include drought, late melting snow pack and infection by snow blight or the brown snow felt fungus (Tab. 2). Their adverse effects may usually not be compensated by a slightly warmer environment (see also Henttonen et al. 1986; Holtmeier 1993; Almquist et al. 1998; Holtmeier et al. 2003; Holtmeier & Broll 2005; Juntunen & Neuvonen 2006).

On rapidly draining substrates, soil moisture supply for seedlings and young growth may become the critical factor, particularly in dry continental climates. Late-lying snow, as a result of increased precipitation (higher vapour pressure at warmer air temperatures), may prevent new tree generations in maritime regions (cf. Holtmeier et al. 2003). Under warmer climatic conditions more wet snow is likely that will increase the risk of snow fungus infection in the evergreen conifers (cf. Tab. 2). On the other hand, at well-drained sites with late-melting snow, plant growth will start with comparatively rapidly rising temperatures, which means that the quality (warmth and moisture) rather than the length of the snow-free period will control seedling establishment and growth (cf.

Figure 10: Unstable block debris prevents treeline advance on the steep south-facing slopes of Mt Tukuhnikivatz (3805 m) (La Sal Mountains, Utah). Photograph taken by F.-K. Holtmeier, 21 July 1994.

Walker et al. 1999; Weih 2000; Karlsson & Weih 2001). Although milder winters are likely to reduce mortality in seedlings and saplings (e.g., Kullman 2007) they will also bring about an increase of freeze-thaw temperature regimes that may prove extremely dangerous for plants that are not completely covered with snow (e.g., Skre 1988; Gross et al. 1991; Perkins et al. 1991). Dehardening of exposed needles and shoots during warm intervals in the winter weather will increase frost damage.

Treeline advancing to greater altitude will bring about exposure to a much windier environment. As a result, frost drought, deflation and damage caused directly to the trees by strong winds, such as abrasion by snow, ice and sand particles, as well as frost drought are likely to increase as long as tree population is too small to enhance snow accumulation (e.g., Holtmeier 1974, 1985; Dahms 1992; Holtmeier 2003, Holtmeier et al. 2004; Seppälä 2004; Holtmeier 2005a; Kullman 2005b). In the most exposed locations of the treeline ecotone and above, seedling establishment and survival will profit from shelter provided by geomorphic features, i.e. the leeward sides of boulders, solifluction terraces or low ridges, for example (cf. Holtmeier 2003; Resler et al. 2005; Resler 2006). The physiological and mechanical effects of strong winds will prevent the most exposed trees from developing "normal" growth. The advanced tree individuals will reach "tree size" only if they can survive after being decoupled from the relatively warm microenvironment near the ground (Wegener 1923; Holtmeier 1974; Wardle 1974; Dahl 1986; Wilson et al. 1987; Grace 1988, 1989). This will probably change with increasing tree population densities (e.g., Germino & Smith 1999; Germino et al. 2002; Smith et al. 2003; Johnson et al. 2004; see also Fig. 14).

Although continued warming is likely to be followed by an altitudinal and latitudinal
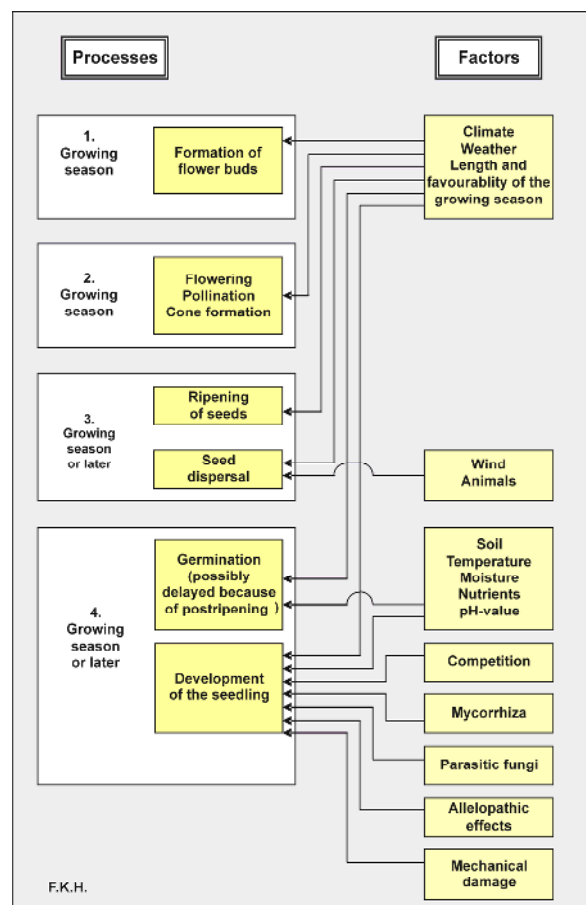

Figure 11: Factors and processes controlling seed-based regeneration at treeline (modified from Holtmeier 1993)

treeline advance extreme events such as drought or severe frosts during the growing season, insect mass outbreaks, and wildfires may cause local setbacks to tree development as has repeatedly happened in the past (cf. Table 2 and Figs. 3, 6). Extreme events, however, and their relative importance for treeline change cannot be predicted. In addition, the after-effects of landscape and site history (see also Halloy 1989) will have unpredictable effects on treeline dynamics in the future. There is no good reason to expect that regional variations in treeline response to the changing climate will be smaller in the future than they were in the past.

The consequences of climate warming for altitudinal treeline on tropical mountains have

Table 2: Factors influencing tree establishment within the treeline ecotone and beyond the present tree limit.

Adverse factors	Beneficial factors
▪ Increase of cold and short growing seasons impeding photosynthetic performance and development of cold resistance	▪ Increase of warm and long growing seasons improving photosynthetic performance and development of cold resistance
▪ Extremely snow-rich winters (may impede tree establishment, particularly in maritime climates)	▪ Snow cover deep enough to provide seedlings and sapling with shelter from climatic injuries and herbivores during winter
▪ Winters with little snow (may cause set-backs to seedlings and saplings, mainly in continental climates)	
▪ Drought (may cause setbacks to seedling establishment, mainly in continental climates)	
▪ Paludification, waterlogging (on flat topography, in depressions and in the active layer)	▪ Balanced soil moisture conditions, sufficient soil moisture supply
▪ Frequent high wind velocities causing physiological and mechanical stress	▪ Low to moderate wind velocities
▪ Late and early frosts	▪ Frost-free growing seasons
▪ Avalanches, snow slides, snow creep	▪ No destructive snow movements
▪ Land slides (e.g., triggered by thawing permafrost)	▪ Stable substrate
▪ Lack of viable seeds	▪ Sufficient viable seeds
▪ Lack of seed beds suitable for germination	▪ Seed beds suitable for germination
▪ Reproduction mainly by layering	▪ Large numbers of viable seedlings
▪ Strong competition of seedlings and saplings with grassland and dwarfshrub vegetation, allelopathic effects	▪ No or little competition of seedlings and saplings with non-arborescent vegetation for light, nutrients, and moisture
▪ High seedling and sapling mortality	▪ High seedling and sapling survival rates
	▪ Facilitation of seedling establishment and survival by increasing tree population (reduced sky exposure and wind velocities)
▪ Overgrazing (wild-living ungulates)	▪ No or moderate grazing (wild-living ungulates)
▪ Insufficient adaptability of the tree species to the changing environment	▪ High adaptability of the trees species to the changing environment
▪ Intense pastoral use	▪ Nor or moderate pastoral use
▪ Pathogenic insects and fungi, diseases	▪ No or little disturbance by pathogenic insects and fungi, no diseases
▪ Severe wildfires	▪ No wildfires
▪ Nutrient deficiency	▪ Unlimited nutrient supply
▪ Over-aging of trees	▪ Recovery of hitherto suppressed mat and table trees by releasing vertical leaders

almost not been considered so far. More frequent and persistent droughts might affect treeline more than would the rise of average air temperature (Rundel et al. 1994). Anyway, this is pure speculation, in particular as geoecological paradigms developed from studies on treelines outside the tropics are unlikely to be of any value for understanding treeline on tropical mountains (Biondi 2001). However, there are good reasons to expect regional variation also in tropical treeline response to changing climate. These include natural factors, tree species represented, past and current anthropogenic influences as well as treeline history. In the Ecuadorian Andes, for example, and also in other tropical mountains, the altitudinal treelines are usually located below the present potential climatic limit of tree growth. They have not kept up with climatic change during the Holocene for several reasons. Besides human impact (mainly pastoral use and fires), insufficient tolerance of tree seedlings to excessive solar radiation appears to be the most important adverse factor. High diurnal radiation loads combined with low night temperatures causing photoinhibition may impede seedlings from becoming established above the usually abrupt forest limits (Bader 2007).

4 Possible consequences of treeline advance

The feedbacks from advancing treelines and the influence of changing treelines on spatial structures will probably be as important as the effects of climatic warming itself. Tree line shift will influence regional and local climates, pedogenesis, mineralization, plant assemblages and animal populations as well as biodiversity (e.g., Haag & Bliss 1974; Holtmeier 1979, Stugren & Popovici 1991; Chapin et al. 2000; Sala et al. 2000; IPCC 2001; Callaghan et al. 2002a; Callaghan et al. 2002b; Bruun & Moen 2003;

Holtmeier 2003; Sjögersten & Wookey 2005; Holtmeier & Broll 2006; Broll et al. submitted). Fragmentation of alpine vegetation and tundra for example, by advancing treeline will increase the risk of species extinction (Moen et al. 2004).

Advance of the altitudinal and northern treeline will also influence human occupation of the forest-tundra transition zone (e.g., Mattson 1995; Vlassova 2002) or in high-mountain valleys (Holtmeier 1973, 1989, 2003). In high mountains, an altitudinal advance of forest would have a stabilizing effect on the snow in what at present are almost treeless avalanche-prone areas. A higher treeline position would improve the protective function of high-elevation forest (avalanches, erosion debris flows, etc.) and thus increase safety for the people living in the mountain valleys. As a consequence of northward shift of the polar treeline (boreal/subarctic forest) considerable economic changes in primary production, for example, may be expected (e.g., IPCC 2001). It seems unlikely, however, that commercial timber production will take place in and beyond the present treeline ecotone in the foreseeable future as predicted by ACIA (2004). Infilling of the treeline ecotone will lag behind climatic change. Consequently, the trees that will become established beyond the present tree limit are likely to grow at too slow a rate for the production of commercial timber.

A northward expansion of the boreal forest of possibly hundreds of kilometres into the tundra will regionally reduce the albedo and increase the roughness of the land surface (e.g., Oke 1987; Bonan et al. 1992; Foley et al. 1994). The release of sensible heat from the low albedo areas to the lower atmosphere is likely to result in a more northern preferred position of the Arctic front along the future polar forest boundary (Pielke & Vidale 1995; Betts & Ball 1997; Harding et al. 2002), which is in direct contrast with previous hypotheses (e.g., Bryson 1966;

Krebs & Barry 1970; Larsen 1971). A comparable significant and large-scale heating-effect from mountain forest advancing to higher elevations cannot be expected, as on steep mountain slopes the increase of the forested area will be relatively small compared with rolling northern peneplains. An advancing northern treeline will also have important implications for the global carbon cycle as the terrestrial carbon sink will probably increase (Grace et al. 2002). However, warming due to decreasing albedo might compensate for higher carbon storage and would thus have an opposite effect (Bachelet & Neilson 2000; ACIA 2004).

Increasing tree populations will bring about deeper winter snow pack. Consequently, snow cover will last longer in the treeline ecotone than in the wind-swept Alpine and in the open tundra (Fig. 12) (Hare 1971; Holtmeier 1978, Hiltunen 1980; Holtmeier 1993; Walsh et al. 1994; Holtmeier 1996; Hiemstra et al. 2002; Holtmeier 2003; Geddes et al. 2005; Holtmeier 2005a). In the treeline ecotone, snow accumulation will also be greater than under dense forest canopies. The greater depth of the snow will increase its insulating properties and snowmelt runoff but decrease the length of the growing season (Fig. 13; see also Liston et al. 2002, therein further references). Soil moisture will remain relatively high all-year round and soils will stay somewhat warmer during the winter as compared to the tundra (Rouse 1984). In an ecotone sparsely covered with trees and tree-stands, i.e. at the beginning of tree invasion, snow depth and its side effects may vary abruptly and widely (Holtmeier 1978, 2003, 2005a; Daly 1984; Holtmeier & Broll 1992; Broll & Holtmeier 1994; Kullman 2005a).

Increased snow pack may facilitate seedling establishment (e.g., Germino & Smith 1999, 2000; Germino et al. 2002; Smith et al. 2003; Bekker 2005), particularly in dry years and in dry regions. On the other hand, long-lying snow may curtail the growing season and increase snow fungus infection (*Phacidium infestans*, *Herpotrichia juniperi*, *Gremeniella abietaina*) of seedlings of evergreen conifers, mainly in wet years and maritime regions (Tab. 2, Fig. 13). Deciduous tree species such as birch, aspen and rowan (e.g., *Sorbus aucuparia*) would not be affected. In addition, mechanical damage to the seedlings and trees by heavy snow loads is likely (e.g., Seki et al. 2005).

Within the treeline ecotones, growing tree population may reduce the risk of summer frost damage by reducing the exposure of seedlings and saplings to intense solar radiation of days following cold nights (e.g., Lundmark & Hällgren 1987; Örlander 1993). Growing tree populations will even out the effects of local topography in the treeline ecotones on wind, snow relocation and solar radiation.

At the northern treeline, reduced wind velocity will exacerbate insect harassment of reindeer and caribou, mainly by warble flies (*Hypoderma tarandi* L.) and nose-bot flies (*Cephenemyia trompe* L.), thus affecting animal condition and survival (e.g., Mörschel & Klein 1997; Hagemoen & Reimers 2002; Holtmeier 2002). In northernmost Europe, this will have negative effects on the reindeer industry economy.

5   Research needs

The changing treeline spatial pattern (Fig. 14; see also Fig. 3) and its regional variation have to be considered to be the main objective of research on treeline position in relation to altitudinal and northward relocation. Regional differentiation of the complex phenomenon "treeline" is needed for speculation on the physiognomic, biological and ecological diversity of future altitudinal and polar treelines. Long-term re-

Figure 12: Treeline ecotone on Rollins Pass (east slope of the Colorado Front Range) in early summer. While the alpine tundra is almost snow-free the treeline ecotone and the forest floor are still covered with snow. Trees invading the present alpine tundra will gradually increase accumulation of drifting snow thus prolonging winter snow cover. Photograph taken by F.-K. Holtmeier, 29 June 1979.

search at the regional and landscape scales within different climatic regions, supported by as many as possible manipulations and other experimental studies in the field and laboratory (see also Callaghan et al. 2002a) appears to be the only way to obtain a deeper insight into the spatial and temporal treeline dynamics and to gain a better understanding of the functional relationships between the many treeline-relevant factors and the fate of the trees (growth, reproduction, survival, etc.).

As to the functional "mechanism" of treeline advance, studies on the functional relationships between regeneration success (survival of seedlings and saplings), for example, and topographically-controlled site conditions are still comparatively rare in the treeline zones and are urgently needed. The varying distribution of soil temperature and soil moisture, as related to topography (runoff, seepage), substrates (texture, soil organic matter), plant cover (transpiration, interception of solar radiation, water use), needs to be studied more intensively at the local and landscape scales.

The physiological response of trees, particularly of seedlings and saplings, to low soil temperatures and related effects have to be studied in different treeline environments. Recently, inhibition of carbon investment due to low temperatures in the rooting zone has been put forward to be the main effect of low soil temperature on tree growth at the altitudinal treeline during the growing season rather than insufficient carbon gain or nutrient limitation, for example (Körner 1998a, 1998b, 1999; Hoch et al. 2002; Körner 2003; Hoch & Körner 2003; Körner & Paulsen 2004; Shi et al. 2006). However, this "carbon sink hypothesis" contrasts with many observations (e.g., Benecke 1972; Ellenberg 1975; Tranquillini 1979; Turner & Streule 1983; Stevens & Fox 1991; Slatyer & Noble 1992;

Sveinbjörnsson et al. 1996; Körner 1994; Karlsson & Nordell 1996; Cairns 1998; Cairns & Malanson 1998; Karlsson & Weih 2001; Hättenschwiler et al. 2002; Smith et al. 2003; Brodersen et al. 2006). It has been speculated that the better trees are adapted to harsh treeline climates the less likely carbon will be a limiting factor to tree growth (Körner 2005). Thus, the carbon-sink hypothesis needs further verification, especially for the establishment and survival of seedlings, before there can be any global generalizations (Smith et al. 2003).

Furthermore, the interactions of climatic summer and winter conditions (outside the tropics) and their effects on seedling establishment and survival need to be more intensely studied in different treeline climates (continental, maritime) before speculating on the possible effects of a warmer environment.

Moreover, consideration has to be given to the ecological properties and requirements of the tree species represented at the altitudinal and polar treelines. In particular, their sensitivity and response to extreme events
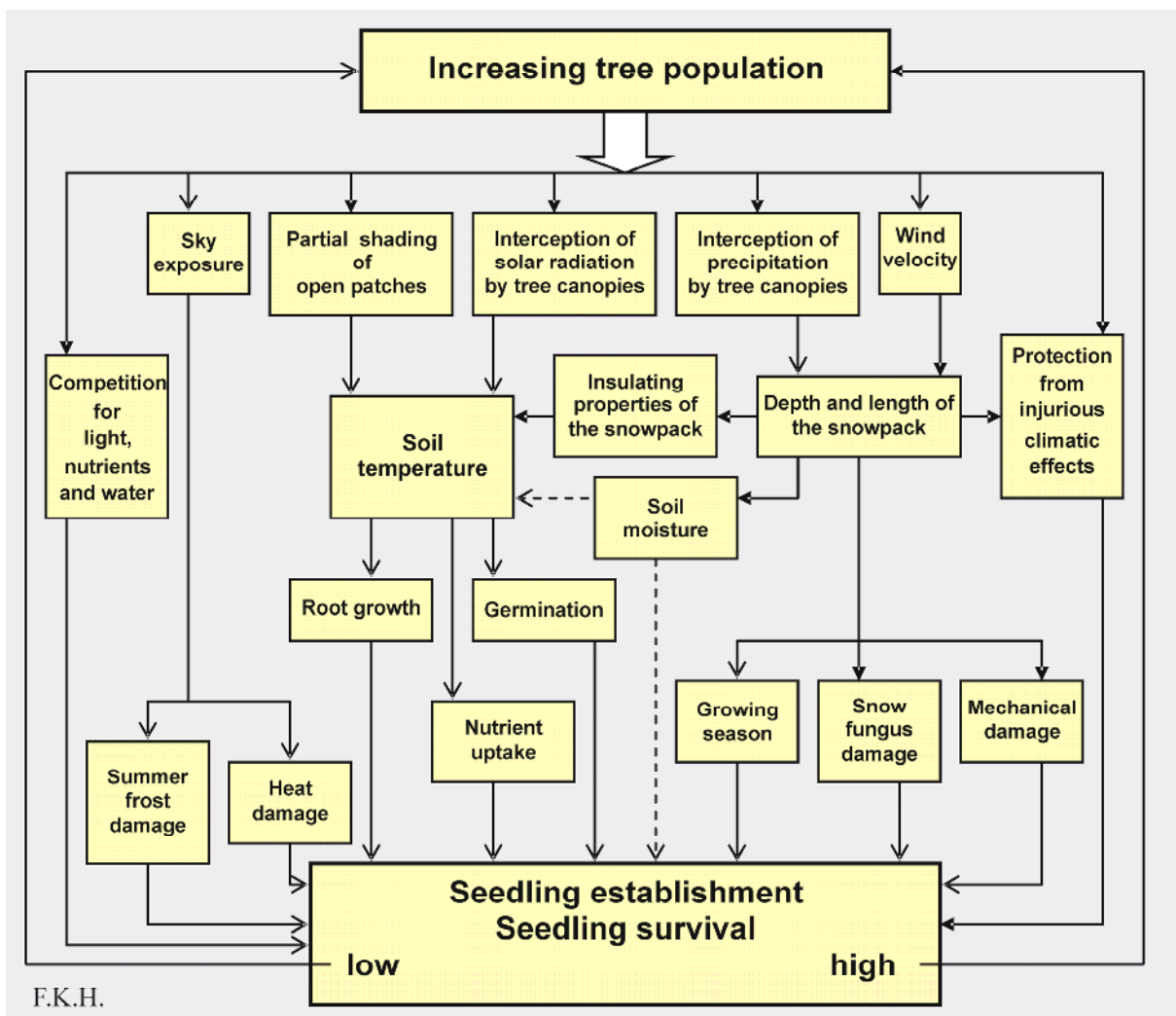

Figure 13: Consequences of increasing tree population within the treeline ecotone and beyond the tree limit. Open arrow heads mean decrease or adverse effects. Filled arrow heads mean increase and beneficial effects. Dashed lines with open arrow head mean positive or negative effects depending on the given situation.
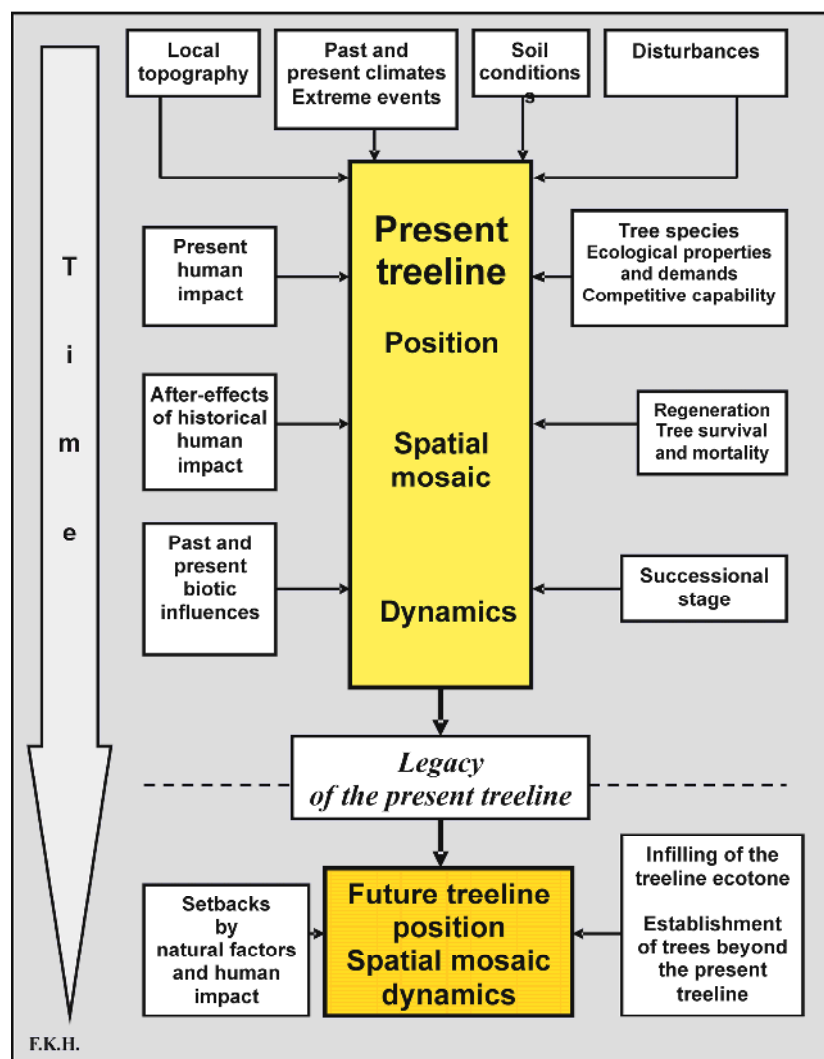
Figure 14: Position, spatial pattern and dynamics of treeline as a result of historical treeline legacy and environmental change.

and a gradually changing environment (physical and biotic) need to be considered. In this context, the adaptability of the tree species to the future environmental conditions will play an important role. Acclimation may lag behind a rapidly changing climate.

Additionally, the distribution pattern of trees within the landscape mosaic, and not least, their competitive ability must be taken into consideration. Diseases, pathogens (e.g., parasitic snow fungi), insect infestations and the effects of wildlife (Holtmeier 2002; Cairns & Moen 2004) have also to be included as agents causing disturbances to

trees and other vegetation. Possible positive and negative effects of disturbances need to be assessed. Disturbances may result in increased tree mortality and decline of tree stands or in intense regeneration and better growth of trees thus influencing the dynamics (e.g., mosaic cycles) within the future treeline ecotones. Mosaic cycles often run counter to the long-term trend in treeline development. Not least, there is a great unsatisfied need for studies on the consequences of changing climate for the treelines on tropical mountains (e.g., Bader 2007).

In principle, remote sensing using space borne techniques (high resolution satellite imagery, orthophotos) are excellent instruments to record the changing spatial and transient structures such as tree canopy cover, kind of vegetation, paludification (e.g., Callaghan et al. 2002b; Crawford et al. 2003), and temporal monitoring of the melt-out pattern in the treeline ecotone at high spatial resolution even in remote and inaccessible regions (e.g., Rees et al. 2002). Remote sensing combined with data from as many as possible field studies and experimental studies in the field and laboratory will contribute to rapidly filling the present local and regional knowledge gaps on spatial and temporal structures of both the northern and mountain treelines and help exploring the functional relationships behind them. Not least, there is a particular need for similar studies on the altitudinal treeline in the tropics and also in the southern hemisphere temperate zone. The worldwide documentation of the treeline spatial patterns and development (e.g., changing tree population density) is an indispensable step in future treeline research rather than further focusing on "better" coincidences between the position of treeline and certain mean air and/or soil temperatures considered to be essential to tree growth.

Modelling will help to assess the possible magnitude of treeline advance to greater altitude and more northern latitude. Scenarios may give an idea of changing spatial patterns of the treeline landscape. In contrast to first-generation "equilibrium models" (e.g., Cramer 1997; Skre et al. 2002), dynamic vegetation models (e.g., Wolf et al. 2007) are able to represent continuous changes by including processes such as establishment, growth, reproduction and mortality, physiological adaptation and competition. Every assessment of treeline response to future climate change must consider the effects of local site conditions and feedbacks of increasing tree population in modulating this

change (e.g., Holtmeier 1985, 1989, 1995a; Luckman & Kavanagh 1998; Holtmeier 2003). So-called "ground truths" are imperative as ever. However, adding all these complexities to the existing models would increase uncertainties in the predictions (Bachelet & Neilson 2000).

Up- and downscaling of empirically found relationships between factors apparently influencing tree growth and treeline have become very popular. The relative importance of the factors varies by the scale of consideration. However, downscaling of statistical relationships existing between the treeline and one or two apparently tree growth limiting environmental factors (e.g., low temperature, aridity) found at the global or zonal scale would produce simplistic scenarios that disguise the complexity of the treeline phenomenon rather than being a contribution to a better causal (functional) understanding. On the other hand, the possibility of upscaling relationships found between soil conditions, tree growth and patchiness of the treeline ecotone is also limited as they depend on the topographical context and thus vary very locally. Soils specific to treeline do not exist. Instead, mosaics of different soil types closely related to the geological substrate, more or less varying with microtopography and plant cover (e.g., grassland, dwarfshrub vegetation) are common to the mountain and northern treeline ecotones (e.g., Burns 1980; Holtmeier 2003; Broll 1994, 1998, 2000).

In short, the complexity of the treeline phenomenon gives us no reason to assume that we will be able to predict reliably how tree growth, tree regeneration and mortality, plant assemblages and animal populations might interact with environmental change in the future. How this "story" will continue may well produce many future surprises for forestry, ecology and for the well-being of our Planet.

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