The Official Journal of the International Association for Landscape Ecology, Chapter Germany (IALE-D)

Landscape Online

International Peer-Review Free-Access Online

Received: 06.11.2009 Received in revision: 07.12.2009 Accepted: 07.01.2010 Published: 02.03.2010

L. Kullman
One Century of Treeline Change and Stability
- Experiences from the Swedish Scandes
Landscape Online 17, 1-31. **DOI:10.3097/LO.201017**

One Century of Treeline Change and Stability - Experiences from the Swedish Scandes

Leif Kullman

Department of Ecology and Environmental Science, Umeå University, 901 87 Umeå, Sweden

leif.kullman@emg.umu.se

Abstract

This paper elaborates and visualizes processes recorded in a recent regional and multi-site study of elevational treeline dynamics during the period 1915 to 2007 in the Swedish Scandes. The purpose is to give a concrete face of the landscape transformation which is associated with the recorded treeline shifts. The main focus is on stand-level structure of past and present treelines and the advance zones, where climate change elicited responses by Betula pubescens ssp. czerepanovii, Picea abies and Pinus sylvestris. All species shifted their treelines upslope by a maximum of c. 200 m in elevation. Most sites, however, manifested changes of smaller magnitudes. This relates to topoclimatic constraints which decouple treeline performance from the macroclimate. The general character of sites which support large and small treeline shifts, respectively, are outlined. The spacing, age structure, growth rates of the tree advance zones are accounted for each of the concerned species. In temporal and spatial detail, the different tree species responded individualistically according to their specific ecologies. Current spread of young seedlings and saplings to increasingly higher elevations in the alpine tundra is particularly highlighted as it may represent the forefront of future treeline advance. It is argued that the current evolution of the treeline ecotone represents a fundamental, although not necessarily entirely unique, reversal of the long-term (Holocene) trend of neoglacial treeline descent.

Keywords:

treeline, tree species line, dynamics, stand structure, climate change, historical perspective

Introduction

A conspicuous landscape ecological consequence of climate change is manifested by elevational shift and structural change of the boundary zone between forest and alpine tundra, represented here by the "treeline" (Kullman 1979, 1997, 1998; Grace et al. 2002; Holtmeier 2003; Holtmeier & Broll 2007; Payette 2007). Such a course of landscape transformation interacts with plant and animal life, geomorphological dynamics, hydrology, and biogeochemical cycles and constitutes a pertinent and prime focus for projective landscape ecological research (Holtmeier 2003; Butler et al. 2009).

Studies at different spatial scales have empirically confirmed different degrees and characters of treeline responses to climate warming and variability (all seasons) over the past century (Hustich 1958; Aas 1969; Kullman 1979; Meshinev et al. 2000; Juntunen et al. 2002; Shiyatov 2003; Esper & Schweingruber 2004; Mazepa 2005; Kharuk et al. 2006, 2009; Danby & Hik 2007; Devi et al. 2008, Harsch et al. 2009). More inertial performance has been displayed and contemplated in other studies (Masek 2001; Lloyd & Fastie 2002; Körner 2003; Dalen & Hofgaard 2005; Rössler et al. 2008). A recent multi-site regional study of elevational treeline change in the southern Swedish Scandes has evidenced various degrees of treeline rise during the period 1915 to 2007 (Kullman & Öberg 2009), when summer and winter temperatures rose oscillatory by 1.0 - 1.4 °C, following upon the "Little Ice Age" cool period ranging about 1300-1850 (Grove 2004). After a first distinct warming peak in the 1930s, temperatures declined marginally for some decades. Around 1988, temperatures lifted again and re-stabilized at virtually the same level as in the 1930s. The present paper seeks to provide a concrete and visual "face" of the "dry" numbers and statistics behind the landscape transformation, which emerges from the above-mentioned study by Kullman & Öberg (2009). This endeavour also integrates earlier case studies performed in the same region by the present author and puts it all in its proper historical (Holocene) context. The detailed methodology and statistics are given in the last-mentioned paper, which is briefly summarized in the following section.

Revisitations (2005-2007) were made at well-identified and circumscribed sites (elevational transects), with baseline data from 1915 and 1975 (Smith 1920, Kullman 1979, 1981a, 1986a). The pattern of sites, as established by Smith (1920), is based on the elevation of the treeline at each 2-5 km kilometer along the mountain valleys in the study region. A main result of the most recent survey was that the treeline of Betula pubescens ssp. czerepanovii (mountain birch), Picea abies (Norway spruce) and Pinus sylvestris (Scots pine) had ascended in elevation by a common maximum of c. 200 m. This was very close to the theoretical prediction, based on a lapse rate of 0.6 °C temperature change per 100 m altitude. At finer spatial and temporal scales, however, the treeline responses were more variable and species-specific, with averages (1915-2007) between 70 and 90 m (Table 1).

Table 1. Species-specific magnitudes of altitudinal treeline shifts during different periods of time.
Source: Kullman & Öberg (2009).

	Altitudinal shift (m) Mean ± S.D. (range)		
Treeline	1915-1975	1975-2007	1915-2007
Birch	45±35 (0-150)	22±25 (-15-110)	68±45 (0-195)
Spruce	47±38 (0-145)	43±45 (0-165)	90±56 (0-220)
Pine	22±27 (0-105)	53±40 (0-175)	75±43 (0-180)

It is clear that the sensitivity to climate change was substantially modulated and constrained by local topoclimatic conditions. Prior to 1975, birch and spruce advanced more rapidly than pine. Thereafter, pine has taken the lead and appears in the long run relatively most suited to benefit from a warmer and drier climate.

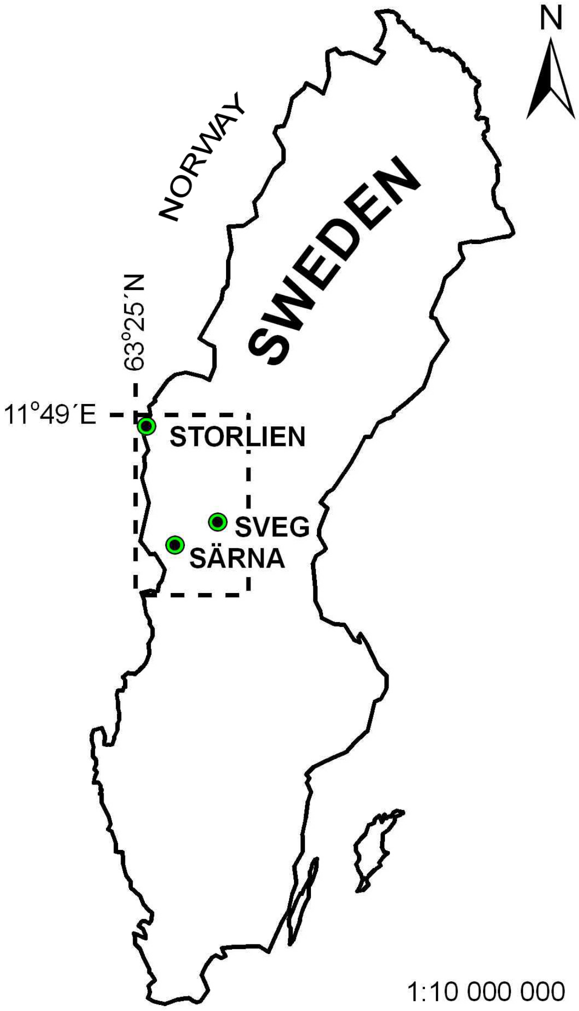

Figure 1: Map showing the study region in Mid-Central Sweden.

Study region

The present study mainly concerns the southern Swedish Scandes, (63°25 to 61°05´N; 12°03´to 13°11´E) and provides results from a monitoring program encompassing more than 200 sites with baseline data from the early 20th century (Fig. 1).

The treeline is defined as the elevation (m a.s.l.) of the uppermost individual of each species, with a minimum height of 2 m at a specific location. In general, the mountain birch forms a subalpine forest belt and the highest treeline towards the alpine tundra. Spruce and pine treelines are located about 50 and 100 m below, respectively. Typically, high above the treeline, there is the tree species line, which is the highest elevation of the most advanced outposts for each species, irrespective of size.

In some parts of the study region, the upper coniferous forest and the lower mountain birch belt have been subjected to low-density grazing by livestock and some cutting for fire and construction wood during 1-2 centuries prior to the 1940s, after which these practices have virtually ceased. As evident from numerous interviews with older local residents and ground surveys, these activities were most intensive somewhat below the treeline ecotone. Hereabouts, the structure and composition of the virgin vegetation landscape have been slightly altered in some areas (Kullman 1979). Prior analyses have evidenced that the new and higher treeline positions, attained during the past century, are not conditioned by responses to past and present human land use and associated land abandonment (Kjällgren & Kullman 1998; Moen & Lyngstad 2003; Virtanen et al. 2003). This contention is supported by accounts of botanists and geographers working in the study area during the later part of the 19th century and first half of the 20th century (Kellgren 1891, Smith 1920; Kilander 1955). These explicitly state that there was no discernible impact of humans or livestock on the treeline position. Strictly locally, extensive use of natural resources in the upper subalpine belt over the past 2000 years or so is claimed, although ambiguously (cf. Holmgren & Tjus 1996), to have lowered the forest limit more or less permanently (Karlsson et al. 2007). In this respect, the current study region is fundamentally different from many mountain ranges around the globe, where human land use has been much more intense and with a longer history into the past (e.g. Aas & Faarlund 2000; Motta & Nola 2001; Gehrig-Fasel et al. 2007; Rössler et al. 2008; Brynn 2008). Grazing and trampling by reindeer are ubiquitous, chronic and integrated disturbances to alpine and subalpine vegetation, with a history spanning many millennia of mutual adaptation (Nordhagen 1928; Cairns & Moen 2004; Eriksson et al. 2007). Since treeline rise of birch, spruce and pine does not discriminate between areas with and without reindeer (Kullman 2004b, 2005b), there is no reason to invoke reindeer impact as principal drivers in this respect. This is not to say that reindeer have no structural and compositional impact on subalpine/alpine vegetation (cf. Olofsson et al. 2009). However, the treeline position per se is not determined by reindeer action.

General accounts of historical land use in the subalpine/alpine regions of the Swedish Scandes are provided by several authors (e.g. Emanuelsson 1987; Ericsson 2001; Kullman 2005a; Linkowski & Lennartsson 2006; Ljungdahl 2007; Öberg 2009). Further details concerning the study area and its climatic, biogeographic, autecological and paleoecological context are outlined by Kullman (2005a), Bergman et al.(2005), Kullman & Öberg (2009).

Results

Below, the species-specific modes and circumstances of treeline (in a broad sense) change or stability are outlined and related to the topoclimatic heterogeneity which characterizes the mountain landscape. Based on Kullman & Öberg (2009), the focus is on three specific aspects, (1) the treeline proper, (2) the tree species line, (3) the advance zone, i.e. the interval between the treeline in 1915 and the new and higher treeline (if any) prevailing in 2007. Unreferenced statements refer to the last-mentioned paper.

Mountain birch

In its present continuous form, the subalpine birch belt is usually comprehended as a consequence of a cold oceanic/suboceanic macroclimate with a deep and late-lying snow cover. Historically, it owes its existence to neoglacial summer cooling and increase of snow cover over the past 5000-6000 years, when this forest type expanded in the wake of altitudinally receding and increasingly fragmented pine-dominated subalpine forests (Kullman 1995a, 2003, 2004a; Bergman et al. 2005).

In most temporal and spatial scales, the performance of the birch belt is closely related to seasonal snow cover dynamics. Specifically, a thick winter snow pack and a steady supply of melt water from alpine snow fields throughout the summer are prerequisite for the “health” and continued existence of the subalpine birch belt (Hämet-Ahti 1963; Kullman 1981a; Aas & Faarlund 2000).

Sustained life of individual mountain birches also depends on recurrent physical disturbances, which kill the main stems in each clone. If that does not happen before these, by age, have lost the ability to resprout, the individual birch will die. This mechanism contributes to the often sparse birch stands and treeless subalpine heaths, prevailing in flat areas where the potential for frequent snow breakage is relatively low. Thus, frequent disturbances, mediated e.g. by snow or insect outbreaks, are essential for the long-term continuity and vitality of the mountain birch forest (Kullman 1981a; Miles 1978; Haukioja & Koricheva 2000).

Modes and magnitudes of treeline rise

Experiences from extensive aging of individual stems by boring, in combination with historical treeline positional records, make it quite easy to pin point the elevation of the early 20th century treeline with a fairly high degree of accuracy (Kullman 1979). The position is marked by the uppermost large and gnarled trees, often with fissured bark with dark lichens (Fig. 2). In cases where the treeline has raised during the past century, trees growing higher upslope are distinctly slender, with smooth bark and with less epiphytic lichens (Fig. 3).

Figure 2: Old birch tree, representing the treeline position in 1915. The position of the raised treeline, 1010 m a.s.l., is indicated by the arrow. Mt. Mettjeburretjakke 885 m a.s.l. 6 September 2007.

To a large extent, treeline rise over the past century has been achieved by accelerated height growth of old-established individuals, implying a transformation from krummholz, i.e stunted low-growing individuals, to erect arborescent modes. This option is due to an eminent capability for vegetative regeneration by adventitious shoots from individual stem bases and old root stocks (Kallio & Mäkinen 1978), which also makes birch relatively resilient to physical disturbance, e.g. logging and browsing (Hustich 1958; Holtmeier 1974). Even tiny and slender birch trees quite often display disproportionally stout basal trunks, which may yield 150-500 years of age (Kullman 1993a, 2005b) (Fig. 4). Given this ability of long life, provided by vegetative regeneration, it is easily comprehended that some of these birches are residuals from past millennia, when higher temperatures and treelines than today prevailed (Kullman 2003; Kullman & Kjällgren 2006). This mechanism for treeline rise has been termed "phenotypic" (Kullman 2005a) and contributed substantially to the relatively swift upslope response to the first warming pulse of the 20th century, i.e. the 1920s-1930s (Kullman 1979).

Particularly during the past few decades, a second wave of modest elevational birch advancement has been accomplished also by establishment and rapid juvenile height growth of newly seed-established individuals, so-called genotypic treeline rise. That course of change is consistent with a dramatic rise in birch seed viability over the past 20 years (Kullman 2007a).

As indicated above, the extent of treeline rise during the past century and up to the present was highly dependent on the topographical relief, which governs local climates and associated ecological conditions, such as wind exposure, snow cover and soil depth. The largest upshifts, i.e. around 200 m occurred in long, sweeping, concave and well-watered slopes, with a rugged mesotopography (boulders, crevices and ledges) offering wind shelter and enduring supply of soil moisture from local snow accumulations higher upslope (Fig. 5, 6). Quite frequently the newly raised treeline is situated in steep and rocky terrain that is virtually inaccessible to

Figure 3: Young and rapidly growing birch, constituting the recently elevated treeline, 1010 m a.s.l., at the site depicted in Figure 2.

Figure 4: Left. A birch tree clone with no stems higher than 2 m in the early-20th century, when this site was above the local treeline. Right . Disproportionally stout lower trunks display 150-200 tree rings. Mt. Falkstolen, 925 m a.s.l. 14 September 2009.

reindeer and humans (Fig. 6).This implies that birch trees cannot have been excluded here by prior reindeer grazing or any kind of human activity. This is one line of arguing that treeline rise is a natural, climatically forced process.

Over most of the mountain landscape, where a more simple topography prevails, treeline ascent was to some degree decoupled from the regional climate and less extensive than the theoretical prediction and locally even non-existing. Therefore, the average treeline rise over the entire study region was much smaller than 200 m. A value around 70 m is more representative of the modal situation (Kullman & Öberg 2009). It is an intriguing question whether sites with no or insignificant treeline advance have remained analogously inertial during earlier parts of the Holocene.

In slopes with sub-optimal rise, birch expansion has, as a rule, been halted where wind-exposure abruptly exceeds a certain threshold in the terrain and snow deflation becomes aggravated. This constraint may become acute in association with some topographic discontinuity, i.e. a more or less abrupt transition from concavity to wind-exposed convexity (Fig. 7. In fact, wind appears as one of the most important factors which sets and forms the local treeline and its structure (Holtmeier 2003; Seppälä 2004). Notably, certain paleoecological data from the Norwegian Scandes suggest that strong winds have become an increasingly restricting agent throughout the Holocene (Paus 2010).

During the period after 1975, the pace of birch treeline rise has declined relative to the preceding 60 years and relative to spruce and pine. This is particularly evident on south-facing slopes and in those parts of the study area with the relatively most dry and continental climate regime. In these settings, treeline birches are frequently losing vitality, which manifests as drying and dying of individual stems and branches and lack of height increment (Fig. 8). Obviously, these phenomena relate to increased drought as late-lying snow patches have tended to disappear earlier during the summers of the past 15-20 years (Kullman 2007a,b).

Figure 5: Concave slope morphology offers optimal conditions for treeline rise in near-equilibrium with regional evolution of the thermal climate. This landscape was entirely treeless in the early-20th century. Subsequently, the treeline has shifted 130 m upslope. Mt. Lillskarven, 1020 m a.s.l. 16 July 2006.

In more oceanic regions, the birch trees have usually become more vital, with higher individual stems and denser canopies relative to the mid-1970s (Fig. 9). As a consequence, the stands now appear denser.

Figure 6: View of the uppermost section of the same type of slope as shown in Figure 5. A particularly complex geomorphology offers ideal preconditions for substantial treeline advance (190 m). Mt. Lillstendaslfjället, 1070 m a.s.l. 18 September 2006.

As a rule in the entire study region, the treeline birches, which were assessed in 2007 and compared with photographs from the mid-1970s (Kullman & Öberg 2009) have produced virtually no seed-based offspring in their nearest vicinity during the past 30 years. More than lack of viable seed (see above), this circumstance reflects the strong patchiness of specific microscale conditions for the success ("safe sites") and sustained life of the mountain birch (Fig. 10).

A notable aspect of the treeline rise after 1975 is that some new treeline markers seem to be of hybridogeneous origin, with morphological leaf characteristics of both Betula pubescens ssp. czerepanovii and Betula nana.

Higher tree species line

At several localities, the tree species line is located more than 500 m above the treeline (Kullman 2004 a,b, 2007a,b). Young birch seedlings (10-20 years old) have become sparsely established in sheltered sites with ample snow cover, in some cases even close to receding fronts of high-alpine glaciers (Fig. 11).

Likely, much of these 500 m represents a recent advance of the tree species line (Kullman 2007a), which has reached well into the mid-alpine belt. In the early- and mid-20th century, birch saplings and low shrubs (krummholz) rarely existed more than 100 m above the treeline (Smith 1920; Kilander 1955). As indicated above, some of these individuals constituted the basis for subsequent treeline rise. The present-day upshifts of the tree species line to extremely high relative elevations is a widespread phenomenon, reported also from the northernmost Scandes (Karlsson 1973; Sundqvist et al. 2008).

The common and swift expansion of the tree species line indicates that there is little reason to take dispersal limitation into account when projecting future elevational progression of birch vegetation. Findings of birch seeds on snow patches, 600 m above the treeline (Smith 1920) further substantiates this contention. This upshift has taken place despite intensive reindeer grazing (Fig. 12). At several sites, solitary birches, 1-1.5 m high, now occur some tens of meters above the treeline, indicative of potential further rise in a near future.

Figure 7: Over the past 100 years, the treeline has shifted 65 m upslope in this landscape. This implies that the upper half of the forest band did not exist in the early-20th century. Further treeline rise is virtually prohibited by the abrupt transition to wind-exposed and snow-poor terrain right at the current treeline position. Mt. Hårdeggen. 5 August. 2006.

ISSN 1865-1542

Figure 8: Left. The treeline of birch by the mid-1970s (1115 m a.s.l.), when it had advanced by 160 m since 1915. Right. Typically for the situation in continental areas after 1975, stem mortality is unbalanced and there is virtually no individual size increment. Mt. Brattriet. 22 August 2006.

The recent advance of the tree species line is paralleled by increased alpine plant species richness, including upshifts and increasing abundance of several boreal plant species, e.g. Epilobium angustifolium, Cornus suecica, Linnaea borealis, Melampyrum sylvaticum, Trientalis europaea, Juniperus communis, Anthyllis vulneraria, Maianthemum bifolium, Oxalis acetosella (Kullman 2007a,b). In addition, the relative proportions of dwarf shrub heaths and alpine grasslands have increased in the low alpine zone throughout the past century (Kullman 2002, 2004c, 2007a).

Structural patterns in the advance zone

This zone, which was entirely treeless alpine tundra shortly prior to 1915, is now sparsely and patchily populated by birch trees. Closer inspection reveals that some peat and humus hummocks contain subfossil wood remnants, indicating prior existence of sparse birch stands, most which seem to have succumbed in response to the cold conditions prevailing during the Little Ice Age (Kullman 2005c). Analogous retrogressional processes are described from northern Finland (Holtmeier & Broll 2006) and south-central Norway (Paus 2010).

Nearest above the treeline markers of the early-20th century, uniformly younger stems have transformed the prior alpine tundra to a narrow band of birch stands with variable density (Fig. 13). Predominantly, the ground cover within these stands is characterized by Vaccinium myrtillus heaths. Only rarely have more extensive birch wood emerged above the former treeline and virtually never has the advancement of closed forest reached the same elevation as the new and raised treeline. Thus, after a century of oscillatory climate warming, there is no evidence of any major elevational expansion of birch forest into previous alpine tundra (Kullman 1990) (Fig. 14). The relatively small shift of the upper range of closed forest, as evidenced also in parts of the Norwegian Scandes with insignificant prior land use (Moen & Lyngstad 2003; Rössler et al. 2008), suggests that climate influence on this parameter is subdued and indirect (cf. Enquist 1933), mediated e.g. by mires, boulder screes, naked rocks and semi-perennial snow fields, which precludes the evolution of continuous forest but allows the existence of single trees and small clusters. This was realized already by Smith (1920), who found that the "forest limit", in contrast to the treeline, varied substantially in elevation over short distances in areas with virtually the same climate. Possibly, the large separation of advanced treelines and forest limits is also a matter of time, as forest expansion and infilling has to rely more on dispersal and successful establishment than treeline advance. This is suggested e.g. from the fact that abrupt treelines and minor separation of treeline and forest line are characteristic of situations where the altitudinal distribution of arboreal vegetation remained stable.

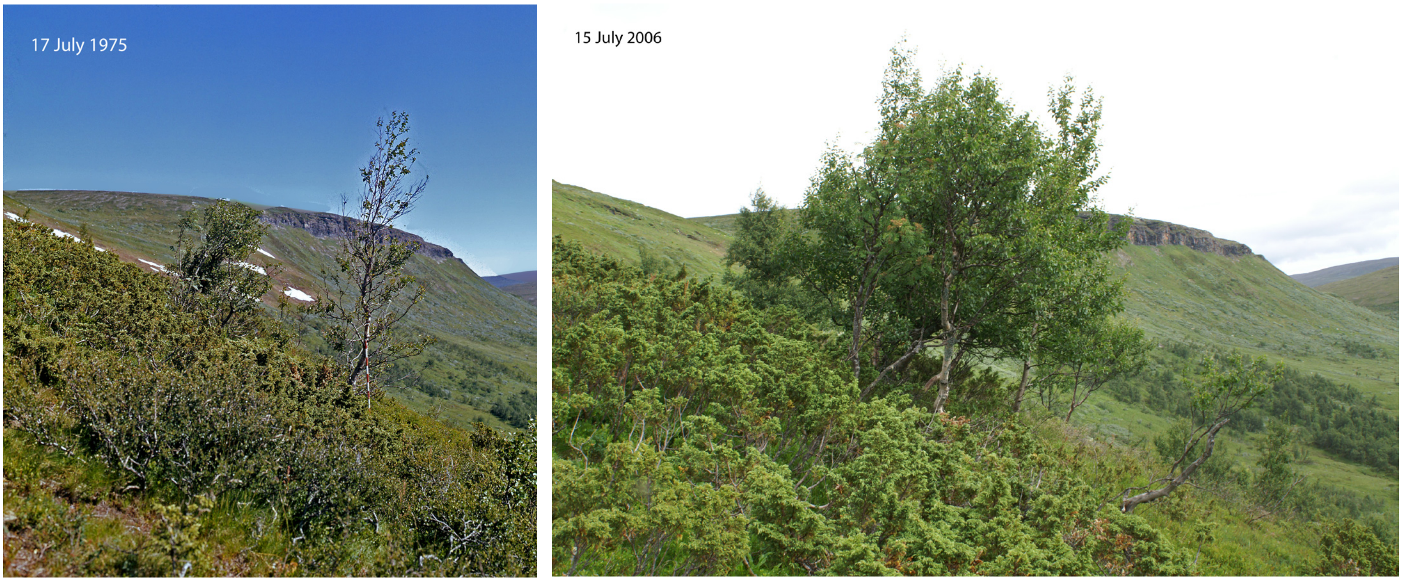

Figure 9. Characteristically, in areas with relatively more oceanic climate, the canopy of most treeline birches has increased in size and density since the mid-1970s. Mt. Hamrafjället, 985 m a.s.l..

In general, the advance zone has the character of an intricate patchwork of widely contrasting habitats, shaped by small-scale toposequences (0.5-10 m) between windswept crests and leeward depressions. As a rule, open spaces predominate, and increase in size with elevation. Solitary trees or small groves consistently occupy minor swales and upper leesides within the microrelief with ample climatic and soil conditions. Typically, the ground cover in the birch spots is dwarf-shrub heath, dominated by Vaccinium myrtillus and Empetrum hermaphroditum. Scattered specimens of snow-bed plants suggest that prior to dwarf-shrub establishment and tree emergence, these sites experienced later snowmelt than today. On most convex surfaces, strong wind erosion, in conjunction with reindeer grazing and trampling, has removed humus and finer mineral soil, which impedes seed-based birch regeneration (cf. Holtmeier 2003; Holtmeier et al. 2003; Kullman 2005c; Anschlag 2008) (Fig. 15). The pattern outlined above is consistent with the well-established fact that reproductive success and radial growth of mountain birch are critically dependent on adequate snow cover, soil moisture and associated nutrient conditions (Kullman 1993a; Kirchhefer 1996; Karlsson & Weih 2001). The critical role of soil water availability, as mediated by wind-conditioned snow drifting is stated by Vajda et al. (2006).

This topographic and edaphic dependence implies that the recorded arboreal adjustments to the new and warmer climate have enhanced a spatial mosaic of trees and alpine tundra, which is unique for each slope. The pattern varies between diffuse dilution zones with mosaics of single trees, ribbons, "fingers" along furrows

Figure 10: Young birch tree growing in a minor depression with more ample snow and moisture conditions than in the surrounding wind-exposed heath. Mt. Tjalmetjallentjakke, 890 m a.s.l. 29 August, 2006.

and tree “islands” in shallow depressions (Kullman 1979). As a consequence of the strong reliance on vegetative regeneration, these spatial tree distribution patterns are strikingly conservative (Kullman 1991). Complete closure of the tree cover in the advance zone rely on slowly working positive feedback loops by which initial presence of trees and small stands facilitate further evolution of tree cover. Accordingly, and counter to the theory advocated by Hoch & Körner (2003), aggregation of trees, ground shading and associated soil cooling do not seem to be the crucial mechanism behind the treeline phenomenon in general (cf. Malanson et al. 2009). In fact, clustering appears to be a highly beneficial mechanism for sustained tree growth and reproduction at the treeline of mountain birch (Fig. 16). Apparently, the reasons are multiple, including wind shelter, protection from frost desiccation and herbivores, potential for seed and snow trapping (moisture) and absorbing of radiation heat.

Figure 11: Young birch sapling, which has established at the top of a frontal moraine close to the lower margin of the glacier Ekorrglaciären, 1370 m a.s.l. This site is about 500 m higher than the local treeline. 5 September 2003.

Figure 12: Despite heavy reindeer grazing, young saplings of birch and pine have become established on this alpine peak, 300 m above the treeline. Moreover the plant species richness has increased by 156% since the mid-1990s (Kullman 2007a). Mt. Norder Tväråklumpen, 1250 m a.s.l. 9 August 2009.

In lower parts of the advance zone, quite abundant birch recruitment is actively taking place in lee topography, mainly on modestly moist soils in snow bed and meadow plant communities. Excess of late-melting snow precluded establishment, survival and sustained growth of birch prior to the past 20-30 years. Subsequently, infilling by new recruits has become a conspicuous process, particularly in snow-rich north-and east-facing slopes. As a consequence, minor “embryonic” birch stands are forming in the local recharge topography, which causes some patchy densification by shrubs and trees (Fig. 17). This is also a characteristic feature in snow glades within the upper reaches of the subalpine birch forest, below the advance zone (Kullman 2007a,b). These processes are particularly pronounced in the most maritime parts of the study area, but virtually non-existing in more continental settings (Kullman 2004b), where late-lying snow did rarely constrain the establishment of birch in the past. Consequently, the birch is developing an increasingly “geriatric” age structure in the latter region where it appears to be slowly losing ground (Kullman 2004b). In a hypothetical case of continued warming, this process is likely to become more ubiquitous as late-summer soil drought would come to prevail also in regions, which today harbour large snow patches in the late summer. On these premises, the mountain birch forest becomes increasingly fragmented and the advance zone remains open. Indications that such a trajectory

Figure 13: Typically in the advance zone, minor tree stands and copses occur in a mosaic with alpine dwarf-shrub heath. This sub-belt extends just some tens of meters above the old treeline. The new treeline (arrow) has the character of isolated outliers, in this case 140 higher than the treeline in 1915. Mt. Getryggen, 835 m a.s.l. 15 July 2009.

is already under way are provided by observations of reduced vitality of well-established and mature birches on dry, flat and convex surfaces, where drought effects are likely to show up first (Kullman 2007b; Öberg 2008). In contrast, birches established in more snow rich, concave and steep terrain do frequently display increasing crown density and height (long annual shoots). Quite commonly, birch stems in these slopes, and which manifested a treeline rise in response to the warm 1930s, have recently reached a stature when they easily break close to the base by the weight of snow. Typically, the broken stems are replaced by basal shoots and the continued individual survival is rarely threatened (Fig. 18). As indicated above, this mechanism is a prerequisite for the vigour and long-term continuity of the birch belt.

Norway spruce

As a rule, spruce is the dominant tree species in the upper forest adjacent to the subalpine birch forest belt. This is mainly and ultimately a consequence of a relatively more humid and snow rich climate compared to lower elevations, where pine and spruce alternate as late-successional dominants in the boreal forest landscape. Spruce usually prefers mesic or moist sites with a sufficient and stable snow cover, moving soil water and freedom of drought during the early summer (Schmidt-Vogt 1977; Tallantire 1977). It is rarely established in pronouncedly dry sites with a thin and fluctuating snow cover, causing severe and prolonged seasonal ground freezing or frequent freeze-thaw cycles. During periods of years with these kinds of winter conditions, seed regeneration is zero and mature treeline spruces suffer from extensive needle loss and even stem mortality. The individual spruces usually survive these harsh periods and recover when more favourable conditions return (Kullman 1997, 2007a).

Modes and magnitudes of treeline rise

The spruce possesses an eminent capability to regenerate vegetatively (Kallio et al. 1971) and the majority

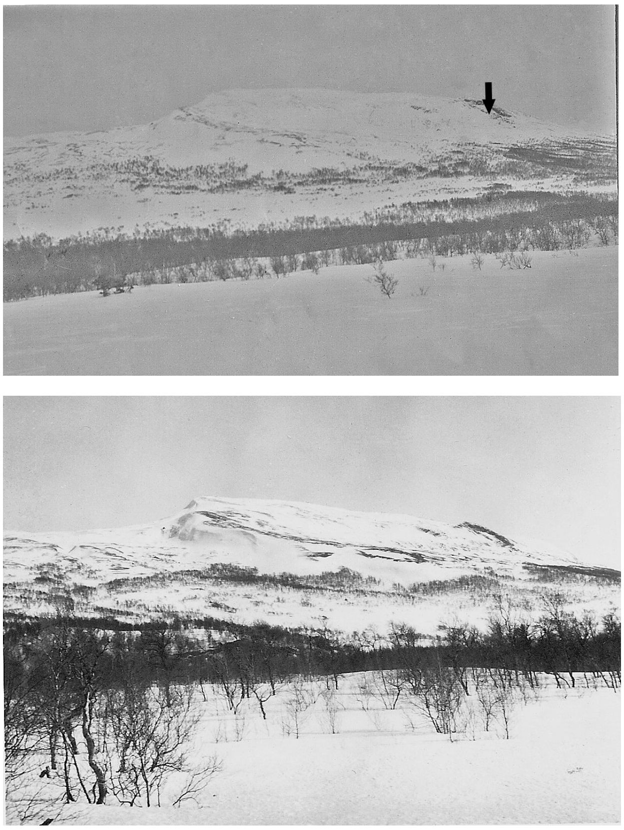

Figure 14: Upper. Mountain side with a fairly sharp "forest line", coinciding with the treeline. Photo by Harry Smith. 14 April 1914. Lower. Approximately the same view 18 April 2007. The upper forest band has become denser and the "forest line" may be somewhat higher. Although not visible here, the treeline (arrow) has advanced substantially and is currently 125 m higher than in 1915. Mt. Mettjeburretjakke.

Figure 15: Birch regeneration is impeded on wind-exposed terrain features, where plant cover, humus and fine mineral soil is constantly removed. Quite frequently, wind erosion and reindeer trampling exposes megafossil birch remnants from stands which prospered here during the Medieval period and succumbed during the Little Ice Age. Mt. Predikstolen, 930 m a.s.l. 4 July 2008.

(c. 95%) of the spruces which form the present-day (2007) treeline are layering and multi-stemmed (10-30 stems) clones. Living stems with ages ranging between 400 and 600 years are occasionally found (Kullman 1995b, 2001, 2009a). The oldest individual spruce clone hitherto dated yielded about 9500 years (Kullman 2001, 2005b, 2009a; Öberg 2008). Thus, some treeline spruces became established in the warmer climate during the early Holocene, when treelines in general were much higher than today (Kullman & Kjällgren 2006). This implies that they have persisted on the same spots during subsequent periods both warmer and colder than at present. Quite frequently, these spruces are bound to the vicinity of irregularly distributed streams and wells, which provide ample moisture and some relief from seasonal ground frost (Kullman & Engelmark 1997; Kjällgren 2003). As climate gradually cooled throughout the Holocene, they transformed from upright trees to prostrate krummholz and persisted in that state for long periods of time. During the past century, most of this ancient pool of stunted individuals has attained tree stature, a process that took its start in the 1930s-40s (Kullman 1986a). Thus, treeline rise during the past century has been predominantly a phenotypic affair (Kullman 2005a, 2009a). In this way, the treeline of spruce has shifted upslope with a maximum extent of 220 m, since 1915 (Fig. 19).

Figure 16: Stem clustering facilitates survival, growth and reproduction at the treeline. In the present case, a founder tree became established between 1910 and 1920. It has been followed by further recruitment during subsequent decades (Kullman 2007a). Mt. Storsnasen 970 m a.s.l. 18 July 2009.

Figure 17: “Embryonic” birch wood rapidly forming in a depression, where late-laying snow precluded tree growth until the mid-2000s. Intensive reindeer grazing and trampling at this site has not prevented birch establishment. Mt. Getryggen, 795 m a.s.l. 17 July, 2009.

Between the mid-1960s and late-1980s, the centennial trend of temperature rise was temporarily broken and treeline markers and trees in the advance zone responded sensitively to cooler conditions by extensive needle loss and stem mortality. At some sites, the treeline displayed minor phenotypic downshifting for this reason (Kullman 1989, 1997). During the past 20-25 years the thermal trend has turned upwards again and the treeline has frequently advanced to somewhat higher

Figure 18. Left. Birches which have emerged above the treeline position in 1915. By the mid-1970s they had reached a size when they were readily broken by the weight of the snow pack. Right. In recent decades, they have rapidly retained their tree size as new stems have developed vegetatively from the bases of the downed trunks. Mt. Blåhammarkläppen 945 m a.s.l. 10 August 2006.

elevations than prior to the temperature dip. For the same basic reason, most treeline spruces have taken on a fresh green and healthy appearance, with exceptionally long needles and annual shoots (Fig. 19, 20). Frost desiccation injuries, which was previously a conspicuous sight close to the treeline, have been virtually absent over the past 10-15 years (Kullman 2007a). In fact, shoot growth has been so remarkable, that it is not easy to comprehend it solely in terms of rising temperature. Although a somewhat controversial issue (cf. Holtmeier & Broll 2007), "fertilization" by rising CO_2 levels in the atmosphere may have contributed to the documented new and more vigorous state of young cold-marginal trees (cf. Bergh et al. 2003; Ainsworth & Long 2005; Loehle 2007; Idso & Singer 2009). Hypothetically, CO_2 enrichment may also have affected stomatal conductance in a way that may have contributed to the reduced incidence of frost drought desiccation.

Higher tree species line

Older botanical records in this region do not indicate the presence of a tree species line more than 100 meters or less above the treeline (Smith 1920; DuRietz 1942; Kilander 1955; Kullman 1986a). Many of these are old-established krummholz spruces and in this mode spruce may survive more or less indefinitely and at higher elevations than similar morphs of mountain birch (Kihlman 1890; Kullman 2008, 2009a). This presupposes that a complex local topography creates wind protection and snow burial of the canopy (Fig. 21). Saplings of spruce now occur sparsely in the alpine tundra, up to 400-500 m above the treeline. These specimens, with a size of 0.1-0.3 m, have germinated during the past two decades and occasionally they have produced viable seeds (Kullman 2002, 2007a,b) (Fig. 22). Notably, spruce seeds have been found on late-lying snow patches (Smith 1920), virtually as high as the uppermost seedlings recorded in recent years. Thus, in a hypothetical case of future climate warming, dispersal limitation is unlikely to influence the treeline position.

Structural patterns in the advance zone

As mentioned above, the spacing of spruce individuals in the advance zone is conservative and partly a reminis-

ISSN 1865-1542

Figure 19: Vigorously growing spruce which marks treeline rise by 185 m since 1915. Prior to that, it persisted as stunted krummholz for centuries or even millennia. Mt. Härjehågna, 1050 m a.s.l. 12 July 2007.

cence of warmer climates in the past. Historical observations and age analyses indicate that much of the spatial pattern of spruce in the treeline landscape was established prior to the onset of 20th century warming (Smith 1920; Kullman & Öberg 2009). In general, the drought intolerance of spruce implies that the largest densities of spruces occur in north-facing slopes, where soil drought is less likely to occur.

Despite the fact that seed viability of old-established spruces growing in the advance zone has increased substantially since the late 1980s (Kullman 2007a), there is little evidence in general that significant recruitment of new individuals has taken place in the advance zone (Öberg 2008). This may relate to increasing surface dryness in combination with a higher frequency of freeze-thaw cycles, which seems to hamper establishment more than growth and survival of older well-established individuals (Sykes & Prentice 1996). Strictly locally, however, single-stemmed individuals have emerged from seed during the present century (Kjällgren 2003). That is mainly on relatively low mountain outliers, surrounded by an upper coniferous forest rim dominated by spruce and where there is a steady supply of propagule from all directions (cf. Kilander 1955; Kullman 2004b). On some mountains of this kind, particularly at the periphery of the mountain chain, relatively little melt water from late-lying snow at higher elevations exists throughout the growth period and therefore a birch belt is insignificant or even absent (Wistrand 1981, Kullman 2004b, 2005b). On these premises, spruce may form the upper treeline and dominate the forest-alpine tundra ecotone. Apparently, spruce dominates here largely due to the snow-accumulating ability of multi-stemmed high-elevation clones, which provides sufficient local soil moisture. Some of these mountains, with only a small cap of alpine tundra with stunted birch shrubs and some krummholz spruces about a century ago, have become more or less overgrown by predominantly spruce trees during the past century (Fig. 23). In most cases, this process is a restoration to the situation just prior to the onset of the Little Ice Age (Kullman 2004b, 2005d, e).

Many spruces which raised the treeline during the first half of the 20th century suffered heavy crown deterioration (needle loss) during some recent cold decades (1960s-1980s), as outlined above. Most individuals have recovered remarkably over the past 20 years by swift emergence of new tree-sized stems from the old

Figure 20: Spruce tree growing in the zone where the treeline advanced relative to early 20th century. During the past 2-3 decades, annual shoots have been exceptionally long. Mt. Anåkroken, 990 m a.s.l. 1 August 2007.

Figure 21: Upper. Many krummholz spruces growing in the alpine tundra are old-established relicts from warmer epochs in the distant past. In this mode, spruce is the hardiest tree species in the Scandes. Radiocarbon-dated megafossils right underneath the canopy indicate that this individual existed already about 1300 years ago (Kullman 2001). This spruce, which is entirely snow-covered in the winter, was described by Kilander (1955). Its physiognomy has not changed perceivably since then. Lower. In 2004, a tiny sapling was discovered and tagged, about 4 m leeward of the old krummholz spruce. The latter has produced seed filled cones at several occasions during the past decades and is most likely the "mother" of the sapling, which had increased somewhat in size in 2009. Mt. N. Tväråklumpen, 1090 m a.s.l. 1 August 2009.

root stocks (Kullman 2007a) (Fig. 24). This is a transformation which is clearly perceivable at the landscape level (Fig. 25). However, for some individual spruces, foliage decline is still in progress, despite the fact that the conditions which initiated it have virtually ceased. Reasonably, this is because they were deprived of a major part of their photosynthetically active foliage during the latest cool period. As a consequence, the basic positive radial growth/temperature relationship was uncoupled. This has deprived those trees from the ability to benefit from rising temperatures and $\mathrm{CO_2}$ – concentrations. Therefore, they currently fail to support a large unproductive trunk structure (Kullman 1996). Thus, these spruces decline in a feedback loop, which prevails over decades and provides an example of the importance of site history. Only rarely has this course of change led to the death of individuals, since new stems regularly emerge vegetatively from old root stocks. As a consequence of these contrasting changes, the advance zone today is a contradictory mixture of healthy, rapidly growing spruce clones and individuals with different degrees of past and present crown deterioration.

Scots pine

Pine is a shade-intolerant species, which is most competitive and invasive in relatively dry, exposed and snow poor subalpine habitats. During the early Holocene, pine formed the highest treeline towards the alpine tundra in most parts of the Swedish Scandes. The treeline reached at least 500 m higher than about a century ago, when it had descended to its postglacial nadir after many millennia of oscillatory climate cooling, culminating with the Little Ice Age. This has been firmly evidenced by radiocarbon-dated subfossil tree remnants preserved in peat and lake sediments (Kullman 1995a; Kullman & Kjällgren 2006). Pollen data yield a broadly similar view (Bergman et al. 2005).

Modes and magnitudes of treeline rise

The treeline position about a century ago stands out quite distinctly in the landscape as the uppermost strikingly stout, often moribund and wide-crowned trees. Typically these are situated in sparse subalpine birch forest where they appear as solitary trees or small restricted groves, often in local south-facing slopes. These trees were the last survivors at the trailing edge of elevational pine retraction, that had proceeded, with some short breaks, for most of the Holocene (see above). Today, they quite often stand as "mother trees" in the centre of clusters of younger individuals, which have become established during and after the 1930s, in close accord with post-Little Ice Age climate warming (Kullman 2007c) (Fig. 26).

In contrast to birch and spruce, pine does not reproduce vegetatively and therefore the long-term postglacial treeline retreat did not leave behind a pool of well-established millennial-old krummholz individuals, which could rapidly and opportunistically transform into erect trees as the climate started to warm in the early 20th century. This seems to be one important reason behind the relatively sluggish treeline rise during the period 1915-1975 (Kullman & Öberg 2009). Obviously, the first distinct warming pulse of the 20th century (1920s to 1930s) was not durable enough to accomplish genotypic treeline rise, although large sapling cohorts appear to have emerged commonly in the Fennoscandian high mountains (Arnborg 1943; Hustich 1958; Kallio 1975; Kullman 1981b). When the warming had culminated in the early-1940s, the apical meristems of most newly seed-produced saplings came to remain for decades in the hazardous zone just above the snow cover, where the risk of winter desiccation and snow/ice abrasion peaks (Hustich 1958, Kullman 1981b, Holtmeier 2003). Observational data from many parts of Fennoscandia indicate that mortality was high during some subsequent decades (Kallio 1975; Kullman 1981b; Holtmeier 2003). Nevertheless, a fraction of these pines survived the colder period as suppressed and deformed shrubs. Quite often they display multiple branching at the stem bases, indicating that they have suffered repeated dieback by frost desiccation and snow abrasion. Some of these pines have been able to take advantage of the resumed warming, which has prevailed in a virtually unbroken sequence over the past 20 years. Thereby they have frequently grown to normal upright trees and raised the treeline (Fig. 27).

Figure 22: Young spruce sapling growing about 400 m higher in elevation than the local treeline. Similar nearby individuals have produced cones with some viable seeds (Kullman 2002). Mt. Åreskutan, 1370 m a.s.l. 2 September 2006.

Figure 23: Low mountain at the eastern continental periphery of the mountain chain. According to old maps and recent tree aging, this and similar mountains supported caps of treeless alpine tundra in the early 20th century. In this case, spruce is the main colonist. Mt. Fjällskaftet. 22 July 2008.

During the past few decades, earlier snowmelt and drying-out of high-elevation soils have provided preconditions for increased competitiveness and growth of pine to tree size in sparse heath birch forests and locally even high on the slopes above the birch region. Taken together, these circumstances have acted to promote a relatively

Figure 24: Left. Subalpine spruce which suffered almost complete defoliation (frost desiccation) during cold winters of the 1970s. 14 July 1972. Right. During the past few decades it has recovered substantially by emergence of new stems from old root stocks. 16 July 2006.

significant treeline readvance and break of the long-term retrogressive trend which gradually converted wide tracts of the highlands of northern and western Sweden from more or less productive and diverse forest to alpine tundra and subalpine birch forest (Kullman & Kjällgren 2006). A particularly striking landscape-scale phenomenon in this context, is the tendencies for the treelines of pine to supersede those of birch and spruce in the most continental parts of the study area (Kullman 2004b, 2005b) (Fig. 28). As a consequence, a sparse pine belt is emerging on the prior alpine tundra, i.e. a return to the early-Holocene zonation pattern.

The great spatial variability with respect to the extent of treeline rise may relate to the stand heterogeneity of the birch forest matrix, in combination with seed shortage. The importance of the last-mentioned aspect is suggested from the striking clustering of seedlings, saplings and young trees to the vicinity old “mother trees” just below the advance zone (Kullman 2007c) (Fig. 26). Also in other northern hemisphere treeline regions, lack of seeds appears to be a more general obstacle for the evolution of denser high-elevation pine stands (cf. Shiyatov 2003; Holtmeier 2003). Spatial variability with respect to the magnitude of treeline rise is caused also by intensive herbivory on young pines by moose (cf. Stöcklin & Körner 1999)

Indeed it has been a remarkable experience during the past 20 years to find treeline pines of all ages and sizes practically devoid of frost desiccation (Kullman 2007c). This contrasts with the situation prevailing during earlier decades, when a large proportion of the foliage used to be killed each winter/spring (Kullman 1993b, 2007c). As a consequence, treeline pines, both trees and saplings, have displayed an unusually vigorous appearance, with freshly green and long annual shoots and needles, clearly stressing that current climatic conditions, particularly during the winter period, have been highly conducive to pine (Öberg 2008). The role of increasing atmospheric CO_2 concentrations needs further consideration in this context (cf. Idso & Singer 2009).

Higher tree species line

Although in very low frequency, pine seeds are regularly spread long distances on the snow crust. Single seedlings and saplings have established in the alpine tundra 10-20 km from the nearest potential seed sources and 500 -700 m above the local treeline (Kullman 2007a) (Fig 29). At the present day, the majority of these individuals seems to be ephemeral and usually they die by frost desiccation when they start to reach above the critical snow surface (see above).

Scarcity of old-growth krummholz in the alpine tundra relates to the fact that the pine treeline is regularly located far below the alpine tundra and often in a matrix of dense and highly competitive birch or birch-spruce forest.

Under such conditions, the shade-intolerant pine rarely survives long enough to form genuine krummholz. Where this occurs, it is mainly on dry and wind-exposed knolls or rock outcrops with an insignificant soil cover, which precludes the closure of the tree cover. The strict confinement to windy habitats implies that these pines, often with a dense, streamlined canopy and stout trunks, are little externally affected by modest warming. At the lowest elevations, however, some specimens of this category, which have been monitored since the early 1970s, have recently displayed tendencies for more upright growth. This seems to be due to reduced pruning by winter desiccation during the past few decades (cf. Kullman 2007c). In addition, viable seeds have been produced for at least a decade and young saplings are showing up leeside of the old krummholz pines (Fig. 30).

Given that the warming trend of the past 100 years or so will continue, treeline rise is likely to proceed since rapidly growing pine saplings of near tree-size (1-1.9 m) are quite abundant at several sites in a zone 0-50 m above the treeline (Öberg 2008) (Fig. 31).

The newly raised tree species line has reached an elevation, which corresponds to the highest known postglacial treeline position, which was during the early Holocene (Lundqvist 1969; Kullman 2004a, Kullman & Kjällgren 2006).

Figure 25: Upper. Episodic climate cooling during the 1980s conditioned landscape-scale defoliation of high-elevation spruce forests (grayish trees) in the southern Swedish Scandes. On this specific slope, the majority of spruce trees lost more than 60 % of their needles (Kullman 1989). Lower. During the past decade a remarkable foliage recovery has changed the face of the entire landscape. Mt. Täljstensvalen (1989 and 2009). Both images were taken in the early evening with similar light conditions.

Figure 26: Old-established pine (to the right), about 300 years old and marking the treeline about a century ago. It has produced at least three generations of offspring in its close surroundings during the past century. Mt. Storsnasen, 670 m a.s.l. 22 July 2006.

Structural patterns in the advance zone

Within the advance zone, there is a strict spatial polarization of the tree species mixture. Preferentially, pine inhabits the warmest, driest and earliest snow free habitats. At the same elevations, mountain birch dominates sites with more abundant snow cover and moister soils, while spruce occupies more intermediate positions in these respects. Reasonably, this differentiation provides a clue also to the relative success of these species in perspective of past and future climatic changes.

With increasing elevation, pine trees become conspicuously smaller and younger, clearly indicative of a surge of upslope spread. Only rarely has pine managed to become established in steep slopes with abundant snow and associated dense birch forest. In these set-

Figure 27: Left. The pine treeline has advanced by 190 m in elevation since the early 20th century at this locality. This pine germinated in an exposed snow poor dwarf-shrub heath by the late 1930s. Right. Multiple branching at the trunk base demonstrates that this pine suffered repeated dieback during the sapling state. Mt. Solberget, 690 m a.s.l. 25 September 2009.

Figure 28: A sparse belt of pine is evolving atop of the subalpine birch forest belt. Mt. Barfredhågna. 14 July 2003.

tings, competition with birch represents a stronger constraint to pine abundance and distribution than more direct climate impacts (cf. Aas & Faarlund 2000).

The advance zone is the result of episodic infilling with single trees (70-30 years old). These are sparsely scattered in heath birch forests, on outliers of alpine tundra and on mires, with maximum density in south-facing slopes (Kullman 1981b, 1986b). Establishment has predominantly occurred in plant communities dominated by low-growing Empetrum hermaphroditum and Betula nana (Kullman 1981b, 2004b).

Following the first warming peak of the 20th century, the density of the subalpine birch forests increased swiftly. This may have contributed to the relatively slow initial advance of pine (Kullman 1976, 1981b), since a dense birch forest acts as a filter reducing the upslope stream of pine seeds (cf. Holtmeier 1974). During the past few decades, however, when tendencies for soil drought have been enhanced, minor recession of dense subalpine birch forest is discernible, particularly in the most continental regions of the southern Swedish Scandes and as a consequence, solitary pines have successfully spread and established in these settings (Fig. 32). This current trend of pine intrusion into the pure subalpine birch forest also involves expansion deeper into mountain valleys where monospecific birch forests previously prevailed. For example in the Handölan Valley, scattered pine trees can now be found about 8 km further towards the head of the valley than a century ago. This process includes an elevational rise by 65 m (Fig. 33).

Today, most pine trees in the advance zone, including the uppermost treeline pines (see above), look strikingly healthy. They have been growing rapidly (0.2-0.4 m/year) during the past two decades, virtually unchecked by frost desiccation injuries (Kullman 2007c). Several of these specimens have reached reproductive maturity and have produced some offspring in their vicinity (Fig. 32). Just like spruce, a minor fraction of the pine trees in the advance zone are sparsely foliated and some continually lose foliage as a legacy of the cold decades prior to the late 1980s.

Pine stands close to and somewhat below the advance zone show signs of selective logging of living and dead trees by local residents in the early-20th century and earlier. However, in only a few percent of all investigated localities have such indications been found within the advance zone (Kullman 1981b). Traces of forest fires

Figure 29: A few years old pine sapling which has germinated in an exposed glacier forefield, about 700 m higher than the local treeline. Mt. Storsola, 1370 m a.s.l. 5 September 2003.

Figure 30: Left. Pine krummholz, more than 400 years old, growing in an open and wind-exposed spot in the lower subalpine birch belt. During the last decade, a slight tendency for more upright growth can be discerned. Right. At the same time, offspring has been produced leeward of the old and stunted pine. Mt. Storsnasen, 650 m a.s.l. 15 August 2009.

in the form of charred fallen trunks and living trees with fire scars, mostly prior to the 20th century, are quite common up to a position somewhat below the treeline prevailing in the early-20th century. At higher elevations, fire traces are highly exceptional and mostly confined to the most continental part of the study area (Kullman 1981b).

Discussion

As demonstrated by Kullman & Öberg (2009), and further exposed in the present paper, climate warming during the past century has evoked regional treeline rise of all studied species in this part of the Swedish Scandes. Rates and magnitudes were site-specific and treelines advanced more than closed canopy forest.

The treeline, as narrowly defined here, is paralleled by analogous changes of other biogeographic and biodiversity patterns in Scandinavian high mountain regions (Kullman 2007a,b). In other words, treeline change in pristine areas is a robust “bellwether” and indicator of climatically changed plant growth conditions in general.

Despite substantial climate warming and upshift of the respective treelines, during the past century, the high-mountain landscape remains largely unforested. The most conspicuous changes, perceivable at the landscape level, concern the elevations around the treeline positions existing about a century ago. In these settings, substantial stand densification has occurred and prior alpine vegetation and flora affinities have become less prominent (Kullman 1986b, 2005b,c).

The large upshifts of the tree species line for all species here concerned suggest, in contrast to Malanson et al. (2009), that the critical life stages for treeline formation are not seed and seedling stages, dispersal or establishment, but rather the tolerance of the early mature phase to ambient air temperature (cf. Grace et al. 2002). If not, alpine krummholz would not exist and most saplings growing in the alpine tundra could be expected to attain tree-size. That notion is further stressed by the fact that even mature treeline trees suffered from severe dieback and even mortality during some cold

Figure 31: Young and near tree-sized pine growing about 30 m above the local treeline. Mt. Städjan, 975 m a.s. l., 14 July 2007.

decades after the mid-20th century, at the same time as nearby small saplings could be virtually unaffected (Kullman 1997).

Mountain birch and spruce responded more swiftly than pine to the first warming pulse of the 20th century (1920s-1930s). These differences highlight species-specific regeneration modes, in response to the same course of climate evolution. In the case of birch and spruce, the ability of vegetative regeneration from old-age and resource-rich root stocks conditioned a general and opportunistic in situ transformation of old-established krummholz individuals to erect tree forms. Birch was the only species whose treeline upshift and increased prominence in the advance zone relied both on sexual and asexual regeneration. Obviously, this provides both stability and potential for spread, i.e. a valuable asset in a fluctuating neoglacial climate. Pine, which virtually lacks the ability of vegetative regeneration, responded exclusively with seed-based regeneration (genotypic treeline change) and therefore more sluggishly. In contrast to birch and spruce, it had to go through all the early life stages before the tree-forming process could take its start. When the establishment phase was accomplished, the warming peak had already passed and most pines were locked in the hazardous sapling phase for decades to come, if they survived at all. Those who did, however, were well established and could quite rapidly develop into upright tree size over the period of climate warming that took its start in the late 1980s.

During some colder decades after the 1940s, treelines of all species were stabilized and locally even marginally retreating (Kullman 1997). Resumed warming over the past 20 years or so has caused treelines to start rising again. However, the pattern is now quite different, both inter- and intra-specifically, from that prevailing during the earlier expansion phase. The previously so opportunistic mountain birch has lost its role as the leading "mountain climber" in the most continental areas, where vigour of treeline birches has frequently declined since the mid-1970s The reason behind appears to be quite complex, and it may be inferred that increasing soil drought is a prominent component in this respect. This link is suggested from the fact that birch decline is strictly confined to discharge topography, where early drought responses are likely to manifest earliest (Kullman 2007b; Kullman & Öberg 2009). In addition, in some parts of the landscape, the treeline has reached such a high elevation that wind exposure

Figure 32: A solitary pine, which has become established in the birch forest belt. Obviously, it has benefited from local drought-induced birch forest regression. A sparse cohort of small saplings (not visible) has become established within a radius of about 10 m. Mt. Getryggen 750 m a.s.l. 12 August 2009.

and associated factors prevent tree growth at higher elevations more or less irrespective of current and future thermal evolution (cf. Gamache & Payette 2005). In this context it is interesting to note that soil drought and strong winds are discussed as factors delaying the early Holocene establishment of pioneer subalpine birch forests in the southern Scandes (Paus 2010).

Figure 33. Young and vigorously growing pine tree, representing 8 km upvalley and 65 m upslope spread since the early 20th century. Mt. Laptentjakke, 770 m a.s.l. 7 July 2008.

Spruce, is less moisture-demanding than birch and its treeline is usually located in less windy settings substantially below. That may be one reason for a relatively high rate of treeline upshift, also after 1975. Over the same period of time, the pine treeline has advanced much more rapidly than both birch and spruce and relative to the first expansion phase. Obviously, pine is favoured by its greater tolerance of drought and the fact that its treeline is usually situated far below the windy alpine tundra. Concurrently, and most importantly, the relatively large and rapid progression over the past few decades of the spruce and pine treelines, relative to birch, is explained by milder winters and reduced frost desiccation injury (Kullman 2007b,c), which should in principle favour evergreen coniferous species more than broadleaved deciduous species (cf. Kaplan & New 2006; MacDonald et al. 2007). Accordingly, over the past few decades there has been a vague tendency for spruce and pine treelines to approach the birch treeline (Kullman & Öberg 2009). The highlighted importance of winter climate conditions for treeline formation is supported by a global meta-analysis of treeline changes over the past century (Harsch et al. 2009).

It may be speculated that in case of continued warming and earlier complete disappearance of the seasonal snow cover, the birch belt will eventually become largely replaced by conifers. A conspicuous expansion of pine can already be gleaned in the most continental parts of the study region. In fact, pine is the only species, which seems to be able of extensive elevational population progression, when climate gets drier and more snow poor in the summer. Thereby it may accomplish genuine treeline rise (genotypic) and spread into existing sparse birch stands as well as colonization of alpine tundra.

In the relatively most maritime regions, the future trajectories are less predictable. In no case, however, is the mountain birch likely to disappear completely from the treeline ecotone. Narrow stands may linger and even advance upslope along particularly snow rich ravines, in scattered snow-accumulating depressions. Possibly, small isolated stands may evolve also in evacuated glacier niches, where birch stands prevailed for some millennia during the generally warm and dry early Holocene (Kullman 2004a), when pine in general formed the forest-alpine tundra ecotone (Kullman & Kjällgren 2006). However, steep environmental gradients within the local topography, particularly with respect to wind and snow cover, imply that sites available for establishment of birch stands will be restricted in size in the alpine landscape above the present treeline position. This, in combination with extensively unfavourable edaphic and orographic condions, precludes broadscale upslope forest spread in a potentially warmer, although not necessarily less windy, future. Thus, in perspective of recent experiences of high-mountain tree performance, there is virtually nothing to suggest that in a warmer climate, birch forest expansion will swamp and homogenize most of the present-day alpine tundra, as simplistically speculated (Moen et al. 2004). On the contrary, a likely consequence will be increased habitat heterogeneity as small birch groves and solitary trees will break the monotony of the alpine tundra. Neither are there any indications that the birch expansion during the past century has conditioned any competition-induced decrease in plant species richness (Kullman 2007a, b, 2009b; Sundqvist et al. 2008). In fact, boreal plant species, e.g. Anemone nemorosa and Chrysosplenium alternifolium, have invaded minor birch groves which became established in the advance zone during the past century (Kullman 2007a). Thus, on the balance of existing empirical data, there is no rational ground for fearing that future treeline rise would cause a general impoverishment of high mountain biodiversity (Kverndal et al. 1990; Idso & Singer 2009; Kullman 2009b). More trees and plant species are exponents of higher primary production and also add to ecological and geomorphic stability and resilience (Körner 2003; Kullman 2009b). In general, the mountains have become greener, more productive and biologically richer during the past century (Kullman 2009b).

When viewing maximum pine treeline advances by c. 200 m (Kullman & Öberg 2009) within the total range of Holocene treeline shifts, as reconstructed by megafossil wood remains (Kullman 2001, Kullman & Kjällgren 2006), it could be inferred that the maximal raised treeline of pine is higher than ever during several past millennia. Obviously, this reflects a fundamental reversal of a multi-millennial (neoglacial) trend of summer cooling and decreasing seasonality, ultimately driven by the orbitally forced reduction in summer insolation (Kullman 2004b; Kullman & Kjällgren 2006). This phenomenon is consistent with observational data from various parts of the world, showing e.g. that some mountain glaciers are currently less extensive than any time during the past 5000 years or more (Solomina et al. 2008; Koch et al. 2006; Kullman 2004a; Bakke et al. 2008). However, in perspective of the disclosed strong spatial variability of recent treeline responses over the past century (Kullman & Öberg 2009), it cannot be ruled out that some short-term episodes of high treelines have been missed by the long-term pine treeline record. For example, the Medieval period (around 1000 years ago) appears to have displayed a distinct thermal peak and climatic conditions highly conducive to prolific tree growth in the North and at high elevations in the mountains (e.g. Hiller et al. 2001; Huldén 2001; Shiyatov 2003; Grudd 2008; Kullman 1998, 2003, 2005d; Loehle 2007; Idso & Singer 2009). This is explicitly highlighted by the fact that climate warming over the past century has not been sufficient to re-establish entirely the stand structure that prevailed during the Medieval period and which was disintegrated by Little Ice Age cooling (Fig. 34). In some respects, the current structure and composition of the treeline ecotone still bears more influence of the Little Ice Age cooling than with the current warmer phase. Accordingly, the long-term treeline history needs further study until this issue has reached a confidence level which allows more definite opinions. For that purpose, paleotreeline research should selectively focus on those sites where the treeline proved to be most responsive and showing the largest upshifts during the past century (Kullman & Öberg 2009). Presumably, that would improve the

Figure 34: By 1915, this was a treeline site with only a few tiny pine trees growing in a matrix of alpine tundra (Kullman 2005d). During the Medieval period, a dense stand prevailed here, as indicated by radiocarbon dated megafossils (foreground). It was gradually exterminated throughout the Little Ice Age. Reforestation during the past century has only succeeded in the least exposed part of the site. Mt. Storsnasen, 670 m a.s.l. 24 June 2009.

time resolution of the treeline history and make it an even sharper paleoclimate proxy. Moreover, Holocene treeline change may be largely a question of changed (declined) seasonality, which should impose species-specific treeline performances. For example and based on the principle of uniformitarianism, it could be suspected that the long-term pine treeline history involves a strong link to snow cover evolution. Thus, definite interpretations of treeline history in terms of climate change have to await birch and spruce treeline chronologies of similar quality as the one available for pine.

It is to be noted that the treeline trends outlined above should not be uncritically extrapolated into the future, since a deterministic model integrating natural and human-driven climate change is still elusive (e.g. Karlén 2008; Idso & Singer 2009). Moreover, species interactions, herbivory (e.g. moose) and diverse feedback mechanisms are complex and poorly understood (cf. Holtmeier 2003; Vajda et al. 2006). Additionally, many climate-driven growth, reproduction and population processes are certainly non-linear, which further complicates projections (Holtmeier 2003; Loehle 2007; Kullman 2007a). In this context it also needs to be stressed that progressive treeline changes, which evolved during decades (position, biomass and structure), can become rapidly eradicated by just a few exceptionally cold years in the future (cf. Kullman 1989, 1997; Holtmeier & Broll 2007). Only time will show whether recent treeline advancement is just a response to a natural climatic caprice or the onset of an alledged new geologic era, the Anthropocene.

Acknowledgements

This study was defrayed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS). I am most indebted to Lisa Öberg and two anonymous reviewers for constructive comments on the manuscript.

References

Aas, B. 1969. Climatically raised birch lines in southeastern Norway 1918-1968. Norsk Geografisk Tidskrift 23, 119-130. doi:10.1080/00291956908542805

Aas, B. & T. Faarlund 2000. Forest limits and the subalpine birch belt in North Europe with a focus on Norway. AmS-Varia 37, 103-147.

Ainsworth, E.A. & S.P. Long 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? New Phytologist 165, 351-372. doi:10.1111/j.1469-8137.2004.01224.x

Anschlag, K, 2008. Regeneration und Wurzelsysteme der Fjellbirke im nordfinnischen Waldgrenzökotone. Arbeiten aus dem Institut für Landschaftsökologie Münster 16, Münster.

Arnborg, T. 1943. Granberget. En växtbiologisk undersökning av ett sydlappländskt granskogsområde med särskild hänsyn till skogstyper och föryngring. Uppsala.

Bakke, J., Lie, Ø., Dahl, S.O., Nesje, A. & A.E. Bjune 2008. Strength and spatial pattern of the Holocene wintertime westerlies in the NE Atlantic region. Global and Planetary Change 60, 28-41. doi:10.1016/j.gloplacha.2006.07.030

Bergh, J., Freeman, M., Sigurdsson, B., Kellomäki, S., Laitinen, K., Niinisto, S., Peltola, H. & S. Linder 2003. Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries. Forest Ecology and Management 183, 327-340. doi:10.1016/S0378-1127(03)00117-8

Bergman, J., Hammarlund, D., Hannon, G., Barnekow, L. & B. Wohlfarth 2005. Deglacial vegetation succession in the Scandes mountains, west-central Sweden. Stratigraphic data compared to megafossil evidence. Review of Palaeobotany and Palynology 134, 129-151. doi:10.1016/j.revpalbo.2004.12.005

Brynn, A. 2008. Recent forest limit changes in southeast Norway: Effects of climate change or regrowth after abandoned utilisation? Norwegian Journal of Geography 62, 251-270.

Butler, D.R., Malanson, G.P., Walsh, S.J. & D.B. Fagre (eds.) 2009. The changing alpine treeline. Developments in Earth Surface Processes 12, 1-197.

Cairns, D.M. & J. Moen 2004. Herbivory influences treelines. Journal of Ecology 92, 1019-1024. doi:10.1111/j.1365-2745.2004.00945.x

Dalen, L. & A. Hofgaard 2005. Differential regional tree line dynamics in the Scandes mountains. Arctic, Antarctic, and Alpine Research 37, 284-296. doi:10.1657/1523-0430(2005)037[0284:DRTDIT]2.0.CO;2

Danby, R.K. & D.K. Hik 2007. Variability, contingency and rapid change in recent subarctic alpine treeline dynamics. Journal of Ecology 95, 352-363. doi:10.1111/j.1365-2745.2006.01200.x

Devi, N., Hagedorn, F., Moiseev, P., Bugmann, H., Shiyatov, S., Mazepa, V. & A. Rigling 2008. Expanding forests and changing growth forms of Siberian larch at the Polar Ural treeline during the 20th century. Global Change Biology 14, 1581-1591. doi:10.1111/j.1365-2486.2008.01583.x

Du Rietz, G.E. 1942. De svenska fjällens växtvärld. Ymer 62, 169-190.

Emanuelsson, U. 1987. Human influence on vegetation in the Torneträsk area during the last three centuries. Ecological Bulletins 38, 95-111.

Enquist, F. 1933. Trädgränsundersökningar. Svenska Skogsvårdsföreningens Tidskrift 31, 145-191.

Ericsson, T.S. 2001. Culture within Nature. Acta Universitatis Agriculturae Sueciae Silvestria, Umeå.

Eriksson, O., Niva, M. & A. Caruso 2007. Use and abuse of reindeer range. Acta Phytogeographica Suecica 87, 1-106.

Esper, J. & F.H. Schweingruber 2004. Large-scale treeline changes recorded in Siberia. Geophysical Research Letters 31, 1-5. doi:10.1029/2003GL019178

Gamache, I. & S. Payette 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography 32, 849-862. doi:10.1111/j.1365-2699.2004.01182.x

Gehrig-Fasel, J., Guisan, A. & N.E. Zimmermann 2007. Tree line shifts in the Swiss Alps. Climate change or land abandonment? Journal of Vegetation Science 18, 571-582. doi:10.1111/j.1654-1103.2007.tb02571.x

Grace, J., Berninger, F. & L. Nagy 2002. Impacts of climate change on the treeline Annals of Botany 90, 537-544. doi:10.1093/aob/mcf222

Grove, J.M. 2004. Little ice ages. Ancient and modern. Volume 1. Routledge, London.

Grudd, H. 2008. Torneträsk tree-ring width and density AD 500-2004: a test of climatic sensitivity and a new 1500-year reconstruction of north Fennoscandian summers. Climate Dynamics 31, 843-857. doi:10.1007/s00382-007-0358-2

Hämet-Ahti, L. 1963. Zonation of the mountain birch orests in northernmost Fennoscandia. Annales Botanici Societatis Zoologicæ Botanicæ Fennicæ “Vanamo” 34, 1-127.

Harsch, M.A., Hulme, P.E., McGlone, M.S. & R.P. Duncan 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12, 1040-1049. doi:10.1111/j.1461-0248.2009.01355.x

Haukioja, E. & J. Koricheva 2000. Tolerance to herbivory in woody vs. herbaceous plants. Evolutionary Ecology 14, 551-562. doi:10.1023/A:1011091606022

Hiller, A., Boettger, T. & C. Kremenetski 2001. Mediaeval climatic warming recorded by radiocarbon dated alpine tree-line shift on the Kola Peninsula, Russia. The Holocene 11, 491-497. doi:10.1191/095968301678302931

Hoch, G. & C. Körner 2003. The carbon charging of pines at the climatic treeline: a global comparison. Oecologia 135, 10-21.

Holmgren, B. & M. Tjus 1996. Summer air temperatures and tree line dynamics at Abisko. Ecological Bulletins 45, 159-169.

Holtmeier, F.-K. 1974. Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht. Franz Steiner Verlag, Wiesbaden.

Holtmeier, F.-K. 2003. Mountain timberline, ecology, patchiness, and dynamics. Kluwer Academic Publishers, Dordrecht.

Holtmeier, F.-K., Broll, G., Mütherthies, A. & K. Anschlag 2003. Regeneration of trees in the treeline ecotone: northern Finnish Lapland. Fennia 181, 103-128.

Holtmeier, F.-K. & G. Broll 2006. Radiocarbon-dated peat and wood remains from the Finnish Subarctic: evidence of treeline and landscape history. The Holocene 16, 743-751. doi:10.1191/0959683606hl968rp

Holtmeier, F.-K. & G. Broll 2007. Treeline advance – driving processes and adverse factors. Landscape Online 1, 1-33. doi:10.3097/LO.200701

Huldén, L. 2001. Ektunnor och den medeltida värmeperioden i Satakunda. Terra 113, 171-178.

Hustich, I. 1958. On the recent expansion of the Scotch pine in northern Europe. Fennia 82, 1-25.

Idso, C. & S.F. Singer 2009. Climate Change Reconsidered: 2009 Report of the Nongovernmental Panel on Climate Change (NIPCC). The Heartland Institute, Chicago.

Juntunen, V., Neuvonen, S., Norokorpi, Y. & T. Tasanen 2002. Potential for timberline advance in northern Finland, as revealed by monitoring during 1983-99. Arctic 55, 348-361.

Kallio, P. 1975. Reflections on the adaptation of organisms to the northern forest limit in Fennoscandia. Proceedings of the Circumpolar Conference of Northern Ecology, Ottawa 1975, 21-37.

Kallio, P., Laine, U. & Y. Mäkinen 1971. Vascular flora of Inari Lapland. 2. Pinaceae and Cupressaceae. Reports from the Kevo Subarctic Research Station 8, 73-100.

Kallio, P. & Y. Mäkinen 1978. Vascular flora of Inari Lapland. 4. Betulaceae. Reports from the Kevo Subarctic Research Station 14, 38-63.

Kaplan, J.O. & M. New 2006. Arctic climate change with a 2 °C global warming: Timing, climate patterns and vegetation change. Climatic Change 79, 213-241. doi:10.1007/s10584-006-9113-7

Karlén, W. 2008. Recent changes in the climate: natural or forced by human activity? Ambio Special Report 14, 483-488.

Karlsson, H., Hörnberg, G., Hannon, G. & E.-M. Nordström 2007. Long-term vegetation changes in the northern Scandinavian forest limit: human impact-climate synergi. The Holocene 17, 37-49. doi:10.1177/0959683607073277

Karlsson, L. 1973. Autecology of cliff and scree plants in Sarek National Park, northern Sweden. Växtekologiska Studier 4, 1-203.

Karlsson, P.S. & M. Weih 2001. Soil temperatures near the distribution limit of the Mountain birch (Betula pubescens ssp. czerepanovii): implications for seedling nitrogen economy and survival. Arctic, Antarctic, and Alpine Research 33, 88-92. doi:10.2307/1552281

Kellgren, A.G. 1891. De skogbildande trädens utbredning i Dalarnes fjälltrakter. Botaniska Notiser 1891, 182-188.

Kharuk, V.I., Ranson, K.J., Im, S.T. & M.M. Naurzbaev 2006. Forest-tundra larch forests and climatic trends. Russian Journal of Ecology 37, 291-298. doi:10.1134/S1067413606050018

Kharuk, V.I., Ranson, K.J., Im, S.T. & M.L. Dvinskaya 2009. Respose of Pinus sibirica and Larix sibirica to climate change in southern Siberian alpine forest-tundra ecotone. Scandinavian Journal of Forest Research 24, 130-139. doi:10.1080/02827580902845823

Kihlman, A.O. 1890. Pflanzenbiologische Studien aus Russich Lappland. Acta Societatis Pro Fauna et Flora Fennica 68(3), 1-263.

Kilander, S. 1955. Kärlväxternas övre gränser på fjäll i sydvästra Jämtland. Acta Phytogeographica Suecica 35, 1-198.

Kirchhefer, A.J. 1996. A dendrochronological study on the effect of climate, site and insect outbreaks on the growth of Betula pubescens coll. in northern Norway. Palaeoclimate Research 20, 93-106.

Kjällgren, L. 2003. Spatial and temporal aspects of tree-limit altitudes in the Swedish Scandes. PhD-thesis, Department of Ecology and Environmental Science, Umeå University.

Kjällgren, L. & L. Kullman 1998. Spatial patterns and structure of the mountain birch tree-limit in the southern Swedish Scandes – a regional perspective. Geografiska Annaler 80A, 1-16. doi:10.1111/1468-0459.00023

Koch, J., Claque, J.J. & G. Osborn 2006. The warmest century of the last 8000 years. In: Price, M. (ed.): Global change in mountain regions. Sapiens Publishing, Duncow, 69.

Körner, C. 2003. Alpine plant life: functional ecology of high mountain ecosystems and their explanation. Springer, Berlin.

Kullman, L. 1976. Recent trädgränsdynamik i V Härjedalen. Svensk Botanisk Tidskrift 70, 107- 137.

Kullman, L. 1979. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes. Acta Phytogeographica Suecica 65, 1-121.

Kullman, L. 1981a. Some aspects of the ecology of the Scandinavian subalpine birch forest belt. Wahlenbergia 7, 99-112.

Kullman, L. 1981b. Recent treeline dynamics of Scots pine (Pinus sylvestris L.) in the southern Swedish Scandes. Wahlenbergia 8, 1-67.

Kullman, L. 1986a. Recent tree-limit history of Picea abies in the southern Swedish Scandes. Canadian Journal of Forest Research 16, 761-771. doi:10.1139/x86-136

Kullman, L. 1986b. Late Holocene reproductional patterns of Pinus sylvestris and Picea abies at the forest limit in central Sweden. Canadian Journal of Botany 64, 1682-1690. doi:10.1139/b86-225

Kullman, L. 1989. Cold-induced dieback of montane spruce forests in the Swedish Scandes – a modern anlaogue of paleoenvironmental processes. New Phytologist 113, 377-389. doi:10.1111/j.1469-8137.1989.tb02416.x

Kullman, L. 1990. Dynamics of altitudinal tree-limits in Sweden: a review. Norsk Geografisk Tidsskrift 44, 103-116. doi:10.1080/00291959008552248

Kullman, L. 1991. Structural change in a subalpine birch woodland in North Sweden during the past century. Journal of Biogeography 18, 53-62. doi:10.2307/2845244

Kullman, L. 1993a. Tree-limit dynamics of Betula pubescens ssp. tortuosa in relation to climate variability: evidence from central Sweden. Journal of Vegetation Science 4, 765-772. doi:10.2307/3235613

Kullman, L. 1993b. Pine (Pinus sylvestris L.) tree-limit surveillance during recent decades, central Sweden. Arctic and Alpine Research 25, 24-31. doi:10.2307/1551476

Kullman, L. 1995a. Holocene tree-limit and climate history from the Scandes Mountains, Sweden. Ecology 76, 2490- 2502. doi:10.2307/2265823

Kullman, L. 1995b. New and firm evidence for Mid-Holocene appearance of of Picea abies in the Scandes Mountains, Sweden. Journal of Ecology 83, 439-447. doi:10.2307/2261597

Kullman, L. 1996. Recent coooling and recsssion of Norway spruce (Picea abies (L.) Karst.) in the forest-alpine tundra ecotone of the Swedish Scandes. Journal of Biogeography 23, 843-854. doi:10.1111/j.1365-2699.1996.tb00042.x

Kullman, L. 1997. Tree-limit stress and disturbance. A 25-year survey of geoecological change in the Scandes Mountains of Sweden. Geografiska Annaler 79A, 139-165. doi:10.1111/1468-0459.00012

Kullman, L. 1998. Tree-limits and montane forests in the Swedish Scandes: sensitive biomonitors of climate change and variability. Ambio 27, 312-321.

Kullman, L. 2001. Immigration of Picea abies into North-Central Sweden. New evidence of regional expansion and tree-limit evolution. Nordic Journal of Botany 21, 39-54. doi:10.1111/j.1756-1051.2001.tb01337.x

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of Ecology 90, 68-77. doi:10.1046/j.0022-0477.2001.00630.x

Kullman, L. 2003. Recent reversal of Neoglacial climate cooling trend in the Swedish Scandes as evidenced by mountain birch tree-limit rise. Global and Planetary Change 36, 72-80. doi:10.1016/S0921-8181(02)00165-0

Kullman, L. 2004a. Early Holocene appearance of mountain birch (Betula pubescens ssp. tortuosa) at unprecedented high elevations in the Swedish Scandes: megafossil evidence exposed by recent snow and ice recession. Arctic, Antarctic, and Alpine Research 36, 172-180. doi:10.1657/1523-0430(2004)036[0172:EHAOMB]2.0.CO;2

Kullman, L. 2004b. Tree-limit and landscape evolution at the southern fringe of the Swedish Scnades (Dalarna province) - Holocene and 20th century perspectives. Fennia 182-202.

Kullman, L. 2004c. A face of global warming – "ice birches" and a changing alpine plant cover. Geo-Öko 25, 181-202.

Kullman, L. 2005a. The mountain taiga of Sweden. In: Seppäla, M. (ed.): The physical geography of Fennoscandia. Oford University Press, Oxford, 163-171.

Kullman, L. 2005b. Old and new trees on Mt. Fulufjället in Dalarna, central Sweden. Svensk Botanisk Tidskrift 99, 315-329.

Kullman, L. 2005c. Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. Arctic 58, 286-294.

Kullman, L. 2005d. Pine (Pinus sylvestris) treeline dynamics during the past millennium – a population study in west-central Sweden. Annales Botanici Fennici 42, 95-106.

Kullman, L. 2005e. Trädgränsen i Dalafjällen. Del. 2. Tandövala-försvinnande sydlig fjällvärld. Länsstyrelsen Dalarnas Län Miljövårdsenheten Rapport 2005(10), 1-25.

Kullman, L. 2007a. Modern climate change and shifting ecological states of the subalpine/alpine landscape in the Swedish Scandes. GeoÖko 28, 187-221.

Kullman, L. 2007b. Long-term geoecological observations of of climate change impacts in the Scandes of West-central Sweden. Nordic Journal of Botany 24, 445-467.

Kullman, L. 2007c. Treeline population monitoring of Pinus sylvestris in the Swedish Scandes, 1973-2005: implications for treeline theory and climate change ecology. Journal of Ecology 95, 41-52. doi:10.1111/j.1365-2745.2006.01190.x

Kullman, L. 2008. Early postglacial appearance of tree species in northern Scandinavia: review and perspective. Quaternary Science Reviews 27, 2467-2472. doi:10.1016/j.quascirev.2008.09.004

Kullman, L. 2009a. Eternal mountain spruces – new light of Swedish forest history. Svensk Botanisk Tidskrift 103, 141-148.

Kullman, L. 2009b. Recent change of alpine vegetation and plant species richness in the Swedish Scandes. Mountain Forum Bulletin 9(2), 20-21.

Kullman, L. & O. Engelmark 1997. Neoglacial climate control of subarctic Picea abies stand dynamics and range limit in northern Sweden. Arctic and Alpine Research 29, 315-326. doi:10.2307/1552146

Kullman, L. & L. Kjällgren 2006. Holocene treeline evolution in the Swedish Scandes: recent treeline rise and climate change in a long-term perspective. Boreas 35, 159-168. doi:10.1080/03009480500359137

Kullman, L. & L. Öberg 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes. A landscape ecological perspective. Journal of Ecology 97, 415-429. doi:10.1111/j.1365-2745.2009.01488.x

Kverndal, A.-J., Elvebakk, A., Jaworowski, Z. & R. Hansson 1990. Virkninger av klimaendringer i polarområdene. Norsk Polarinstitutt Rapportserie 62, 1-118.

Linkowski, W.L. & T. Lennartsson 2006. Biologisk mångfald i fjällbjörkskog. Länsstyrelsen i Norrbottens län Rapportserie 2006(2), 1-71.

Ljungdahl, E. 2007. Det tysta arkivet-om samisk närvaro i fjällen. Jämten 100, 64-71.

Lloyd, A.H. & C.L. Fastie 2002. Spatial and temporal variability in the growth and climate response of treelines in Alaska. Climatic Change 52, 481-509. doi:10.1023/A:1014278819094

Loehle, C. 2007. A 2000-year global temperature reconstruction based on non-treering proxies. Energy & Environment 18, 1049-1058. doi:10.1260/095830507782616797

Lundqvist, J. 1969. Beskrivning till jordartskarta över Jämtlands län. Sveriges Geologiska Undersökning Ser. Ca 45, 1-418.

MacDonald, G.M., Kremenetski, K.V. & D.W. Beilman 2007. Climate change and the northern Russian treeline zone. Philosophical Transactions of the Royal Society B: Biological Sciences 363, 2285-2299. doi:10.1098/rstb.2007.2200

Malanson, G.P., Brown, D.G., Butler, D.R., Cairns, D.M., Fagre, D.B. & S.J. Walsh 2009. Ecotone dynamics: invasibility of alpine tundra by tree species from the subalpine forest. Developments in Earth Surface Processes 12, 35-61. doi:10.1016/S0928-2025(08)00203-4

Masek, J.G. 2001. Stability of boreal forest stands during recent climate change. Evidence from landsat satellite imagery. Journal of Biogeography 28, 967-976. doi:10.1046/j.1365-2699.2001.00612.x

Mazepa, V.S. 2005. Stand density in the last millennium at the upper tree-line ecotone in the polar Ural Mountains. Canadian Journal of Forest Research 35, 2082-2091. doi:10.1139/x05-111

Meshinev, T., Apostolova, I. & E. Koleva 2000. Influence of warming on timberline rising. A case study on Pinus peuce Griseb. in Bulgaria. Phytocoenologia 30, 431-438.

Miles, J. 1978. The influence of trees on soil properties. Annual Report/ Institute of Terrestrial Ecology 1977, 7-11.

Moen, A. & A. Lyngstad 2003. Botaniske verneverdier i Sylan. NTNU Vitenskapsmuseet. Rapport botanisk Serie 2003-5, 1-39.

Moen, J., Aune, K., Edenius, L. & A. Angerbjörn 2004. Potential effects of climate change on treeline position in the Swedish mountains. Ecology and Society 16, 1-10.

Motta, R. & P. Nola 2001. Growth trends and dynamics in subalpine forest stands in the varaita valley (Piedmont Italy) and their relationships with human activities and global change. Journal of Vegetation Science 12, 219-230. doi:10.2307/3236606

Nordhagen, R. 1928. Die Vegetation und Flora des Sylene-Gebietes. I. Die Vegetation. Skrifter Norske Videnskaps-Akademi i Oslo I. Matem.-Naturvidensk. Klasse 1927-1, 1-612.

Öberg, L. 2008. Trädgränsen som indikator för ekologiska klimateffekter i fjällen. Länsstyrelsen Jämtlands län. Miljö/Fiske Miljöövervakning Rapport 2008(01).

Öberg, L. (ed.) 2009. The heart of Härjedalen Sonfjället. National park since 1909. Jämtli Förlag, Östersund.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T. & O. Suominen 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. Global Change Biology 15, 2681-2693. doi:10.1111/j.1365-2486.2009.01935.x

Paus, A. 2010. Vegetation and environment of the Rødalen alpine area, Central Norway, with emphasis on the early Holocene. Vegetation History and Archaeobotany, 19, 29-51. doi: 10.1007/s00334-009-0228-4.

Payette, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. Ecology 88, 770-780. doi:10.1890/06-0265

Rössler, O., Bräuning, A. & J. Löffler 2008. Dynamics and driving forces of treeline fluctuation and regeneration in central Norway during the past decades. Erdkunde 62, 117-128. doi:10.3112/erdkunde.2008.02.02

Schmidt-Vogt, H. 1977. Die Fichte. Band I. Verlag Paul Parey, Hamburg.

Seppälä, M. 2004. Wind as a geomorphic agent in cold climates. Cambridge University Press, Cambridge.

Shiyatov, S.G. 2003. Rates of change in the upper treeline ecotone in the Polar Ural Mountains. Pages News 11, 8-10.

Smith, H. 1920. Vegetationen och dess utvecklingshistoria i det centralsvenska högfjällsområdet. Almqvist & Wiksell, Uppsala.

Solomina, O., Haeberli, W., Kull, C. & G. Wiles 2008. Historical and Holocene glacier-climate variations: General concepts and overview. Global and Planetary Change 60, 1-9. doi:10.1016/j.gloplacha.2007.02.001

Stöcklin, J. & C. Körner 1999. Recruitment and mortality of Pinus sylvestris near the Nordic treeline: the role of climatic change and herbivory. Ecological Bulletins 47, 168-177.

Sundqvist, M., Björk, R.G. & U. Molau 2008. Establishment of boreal forest species in alpine dwarf-shrub heath in subarctic Sweden. Plant Ecology and Diversity 1, 67-75. doi:10.1080/17550870802273395

Sykes, M. & I.C. Prentice 1996. Climate change, tree species distributions and forest dynamics: a case study in the mixed conifer/northern hardwoods zone of northern Europe. Climatic Change 34, 161-177. doi:10.1007/BF00224628

Tallantire, P. 1977. A further contribution to the problem of the spread of spruce (Picea abies (L.) Karst.) in Fennoscandia. Journal of Biogeography 4, 219-227. doi:10.2307/3038058

Vajda, A., Venäläinen, A., Hänninen, P. & R. Sutinen 2006. Effect of vegetation on snow cover at the northern forest line: a case study in Finnish Lapland. Silva Fennica 40, 195-2007.

Virtanen, R., Eskelinen, A. & E. Gaare 2003. Long-term changes in alpine plant communities in Norway and Finland. In: L. Nagy, G. Grabherr, C. Körner, & D.B.A. Thompson(eds.): Alpine biodiversity in Europe. Springer, Berlin, 411-422.

Wistrand, G. 1981. Bidrag till Pite lappmarks växtgeografi. Växtekologiska Studier 14, 1-99.