Tree-limit landscape evolution at the southern fringe of the Swedish Scandes (Dalarna province) – Holocene and 20th century perspectives

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Kullman, Leif (2004). Tree-limit landscape evolution at the southern fringe of the Swedish Scandes (Dalarna province) – Holocene and 20th century perspectives. *Fennia* 182: 2, pp. 73–94. Helsinki. ISSN 0015-0010.

Tree-limit and climate evolution at the southern extremity of the Swedish Scandes have been reconstructed for the entire Holocene and for the past century. The main objective was to test the reproducibility of a similar study further north in the Swedish Scandes. The long-term history relies mainly on radiocarbon-dated megafossil tree remains preserved in peat and mineral soil. The more recent perspective was analysed from age distributions in the most marginal, extant tree populations. *Pinus sylvestris* (pine) immigrated to the study region already during the Late-Glacial, 10,500 ^{14}C yr BP, when it grew in the summit areas of first deglaciated mountains. The pine tree-limit peaked ca. 9200 ^{14}C yr BP, followed by a 345 m gradual descent (summer cooling + land uplift) until about a century ago. Presence of tree species assemblages without modern analogs at high elevations during the early-Holocene, *Pinus sylvestris* (dominant), *Betula pubescens* ssp. *tortuosa*, *Picea abies*, *Larix sibirica*, *Quercus robur* and *Corylus avellana*, strengthens the view of a warm and dry summer climate, although with a different seasonal distribution of incoming radiant energy than today. The long-term natural trend of tree-limit retreat and summer cooling was anomalously broken about a century ago. During the 20th century, the pine tree-limit has shifted 140 m uphill, in congruence with instrumentally recorded summer warming by ca. 1 °C. In a perspective of the entire Holocene tree-limit chronology, the modern tree-limit rise (and climate warming) is anomalous for the past 4000–7000 years. Except for tree-limit rise, recent warming has contributed to changes in the alpine plant cover, e.g. vanishing snow-bed communities, expansion of deciduous dwarf-shrubs, graminoids, and invasion of exotic and thermophilic plant species. Overall, this study has reproduced processes and patterns previously reported further north in the Scandes.

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Introduction

Alpine (upper) tree-limits are potential early indicators of the impact of climate change and variability on ecosystems (Hustich 1958; Kullman 1979, 1997; Meshinev et al. 2000; Moiseev & Shiyatov 2003; Penuelas & Boada 2003). In quantitative terms, these adjustments vary with topoclimatic conditions (Kullman 1979, 2001a). Studies in various parts of the world have used historical tree-limits as proxy paleoclimatic indicators at scales of centuries to millennia (e.g. Karlén 1976; Kullman 1995; Wick & Tinner 1997; Aas & Faarlund 1999; Eronen et al. 1999; Barnett et al. 2001; Payette et al. 2002; Ali et al. 2003). As a consequence of this climatic sensitivity, paleotree-limit records offer an opportunity to view and evaluate the magnitude and rate of instrumentally recorded climate change over the past 100–150 years in a perspective of the entire Holocene (cf. Kullman &

Kjällgren 2000; Kullman 2003a). This approach provides indications of the possible anomalous nature of twentieth-century climate warming, in relation to increasing atmospheric loads of anthropogenically introduced "greenhouse gases" (IPCC 2001a). Moreover, tree-limit history may contribute to a broader general understanding of mechanisms and rates of vegetation adjustments to altered climatic conditions, i.e. a prerequisite for the generation of realistic models concerning vegetation responses to further warming during the rest of the present century.

It is generally recognized that altitudinally-precise (m a.s.l.) tree-limit reconstructions are most reliably achieved from megafossil evidence, i.e. radiocarbon-dated trunks, roots, cones, etc., preserved in peat, lake sediments or on open alpine ground recently vacated by glacier ice and snow (e.g. Aas & Faarlund 1999; Payette et al. 2002). These records provide unambiguous documentation and direct dating of local presence of a tree at a specific altitude. However, megafossil tree-limit chronologies may display temporal gaps, which represent local absence, preservation failure or inadequate sampling (Kullman 1994; Jackson & Booth 2002). Extensive surveys over wide altitudinal ranges for potentially rewarding sampling sites, and an improving skill to find these, can alleviate this "gap-enigma" by bringing together fairly large sample sizes. In this way, Kullman and Kjällgren (2000) accomplished a regional tree-limit chronology (*Pinus sylvestris*) in a sub-oceanic part of the central Swedish Scandes. This chronology is nearly coherent at the centennial-millennial scale and displays a virtually unidirectional descent since the early-Holocene. In addition, this extensive pursuit for megafossil pines has revealed remains of other tree species and other features of the postglacial arboreal landscape history that have been virtually undetected by pollen stratigraphical studies (Kullman 1998a, 1998b, 1998c, 2001b, 2001d, 2002a, 2004b). For example, *Picea abies* immigrated to northern Sweden at least 7000 years prior to earlier belief, and it is also clear that *Larix sibirica* was native to this region during the early-Holocene. These and other analogous discoveries have fundamentally changed general palynological interpretational paradigms concerning immigration and extinction phases within Quaternary vegetation history, i.e. threshold values indicative of local presence (cf. Aas & Faarlund 1999; Segerström & von Stedingk 2003). The paleoclimatic inferences emerging from the megafossil analyses cited above are mirrored by independent reconstructions from other types of sources in northwestern Europe (Jensen et al. 2002; Marchal et al. 2002; Bigler et al. 2003; Väliranta et al. 2003). Nevertheless, there is reason to test further the wider consistency and validity of the above-mentioned tree-limit record and the methodology on which it relies. In particular, the early postglacial tree immigration history and tree-limit evolution merit further scrutiny in wider regions as existing paleoenvironmental data for that period (both in Scandinavia and elsewhere) are sparse and somewhat contradictory (cf. Kullman 2002a; Payette et al. 2002; Ali et al. 2003).

With the above objectives, megafossil tree remains were intensively searched for and retrieved over a wide elevational range in a high-mountain region (Dalarna province), 120–130 km south of the study site embraced by Kullman and Kjällgren (2000). Here, the wood preservation conditions are different, due to a more continental and drier regional climate, implying reduced peat formation at high elevations, absence of glaciers and scarcity of semi-perennial snow-patches. As a consequence, subfossil tree remains may lie exposed on the ground for more than a thousand years after their death (Kullman 1980, 2000). This regional comparison should reveal whether megafossil results are critically dependent on the preservational system.

The following items are specifically focused for consistency with previous megafossil results further north (see above):

(1) Deglaciation and first tree immigration already during the Lateglacial.
(2) Dominance of *Pinus sylvestris* in the forest-alpine tundra ecotone during the early Holocene.
(3) The highest Holocene position of the tree-limit shortly prior to 9000 BP.
(4) Near-linear descent of the *Pinus sylvestris* tree-limit over the past ca. 9000 radiocarbon years.
(5) Tree species assemblages without present-day analogs (the so-called Caledonian forest) dur-

ing the early Holocene, within the current tree-limit ecotone and with members such as *Quercus robur*, *Corylus avellana*, *Betula pubescens* ssp. *tortuosa*, *Betula pendula*, *Picea abies* (henceforth "spruce"), *Pinus sylvestris* (henceforth "pine") and *Larix sibirica*.

(6) 20th century tree-limit rise amounting to > 100 m altitudinally and exceeding the highest level of at least the past 4000 radiocarbon years.

If these features could be broadly reproduced in the present study area, previous results (e.g. Kullman & Kjällgren 2000) and the megafossil approach to paleoclimate reconstruction as such would gain in general relevance and credence.

Study area

The study area, located in Dalarna province of Central Sweden (Fig. 1) is one of the, phytogeographically and paleoecologically, least known mountain areas in the Swedish Scandes. The only comprehensive phytogeographic survey is that by Samuelsson (1917). Except for some older pollen-stratigraphical studies, without radiocarbon dating control (Lundqvist 1951) there is a lack of precise vegetation history data on these subalpine and alpine landscapes.

The present study embraces the most southerly outposts of alpine tundra on high mountains (fells) in the Swedish Scandes. Four of the highest fells, sites 1–4 below, at this extremity of the mountain range are here examined: (1) Mt. Storvätteshågna (max. 1204 m a.s.l.; 62° 07′N, 12° 27′E), (2) Mt. Nipfjället (max. 1192 m a.s.l.; 61° 59′N, 12° 51′E), (3) Mt. Städjan (max. 1131 m a.s.l.; 61° 55′N, 12° 53′E), and (4) Mt. Barfredhågna (max. 1022 m a.s.l.; 62° 04′N, 12° 25′E).

Characteristically, the mountains investigated are smoothly rounded and reach a maximum of 300–400 m above the upper limit of continuous forest. The geological substrate is hard quartzite. Extensive frost-shattered boulder fields cover the peak plateux of most of the highest mountains. At lower elevations, the slopes are clothed with an undifferentiated cover of glacial till. Minor peat accumulations exist near and above the tree-limit, and small lakes, ponds and rivulets are scarce due to early melting of a relatively thin snow cover.

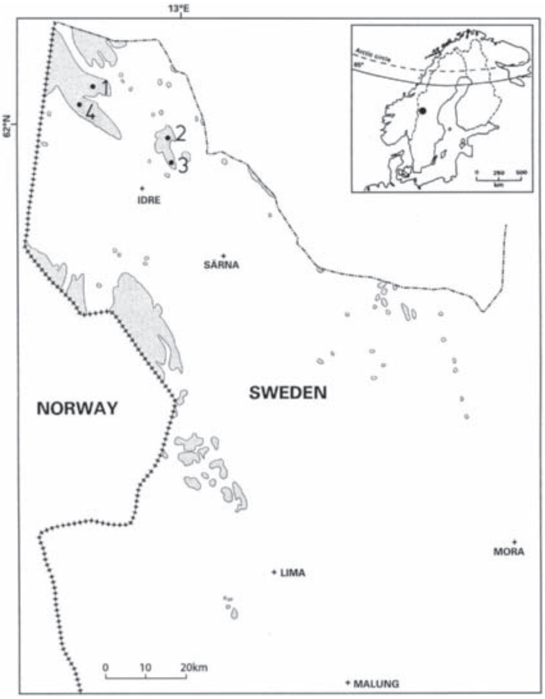

Fig. 1. Location map showing the position of the study sites (1–4) in the "archipelago" of fells (shaded) at the southern fringe of the Swedish Scandes (dot on the small map). The dashed line indicates the northern boundary of the Dalarna province. Modified after Samuelsson (1917).

In contrast to more northerly parts of the Scandes, geomorphic processes such as wind erosion and solifluction are areally relatively insignificant (Lundqvist 1949). Permafrost has not been recorded in this part of the Scandes.

This is the part of the Swedish Scandes that is most distant from the sea. Thus, the climate is moderately continental in character and effective humidity is low in comparison with Scandinavian standards. Temperature norms (1961–90) for January, July and the year are –12.0, 13.0 and 1°C, respectively. Mean annual precipitation amounts to ca. 700 mm. In general, wind strengths are weaker and snow cover thinner and less persistent than in alpine regions further north (Raab & Vedin 1995). During the past 100 years, regional standard meteorological records display distinct warming for all seasons. For two meteorological stations in the region with long-term homogenized data, viz. Falun (200 km SE, 120 m a.s.l.) and Storlien/Visjövalen (160 km N, 640 m a.s.l.), the centennial trend for the period June–August is +0.9 and +1.1 ºC ($p < 0.01$), respectively. Precipitation has increased steadily throughout the past century (Alexandersson 2002) and particularly for the past few decades a tendency for increasing oceanicity is perceivable (Kullman 1997; Tuomenvirta et al. 2000). The overall climate warming trend hides a large inter-annual scatter and the process was slightly reversed for some decades after the mid-20th century (Kullman 1997; Alexandersson 2002).

Where not covered with sterile boulder fields, the highest peaks support a graminoid heath vegetation (*Carex bigelowii*, *Juncus trifidus*, *Festuca ovina*) with variable proportions of reindeer lichens. At lower elevations, sparse, low-growing dwarf-shrub heaths with a bottom layer of reindeer lichens. Locally, with deeper snow cover and moister soil, the heath vegetation is lusher, with a substantial admixture of feather mosses. Small patches of bog vegetation, exist up to 1000 m a.s.l. In comparison with the rest of the Scandes, the alpine flora is strikingly poor in species (Almquist 1949).

The use of the tree-limit as a paleoclimatic indicator necessitates a reasonably narrow and precise definition. Thus, the tree-limit is henceforth defined, for each tree species, as the uppermost elevation (m a.s.l.) of trees with a minimum height of 2 m. Ultimately as a consequence of climatic continentality, the study area comprises the highest tree-limits of *Pinus sylvestris* and *Picea abies* in the Swedish Scandes, 1005 and 1115 m a.s.l., respectively.

The "tree-limit ecotone", i.e. the transition between closed forest and alpine tundra is relatively broad and indistinct, with sparsely scattered trees in a matrix of oligotrophic heath vegetation. A subalpine birch forest belt, that usually makes up most of the tree-limit ecotone in Fennoscandia (Kullman 1981b) is lacking or only fragmentarily developed. Over wide areas, the forest-alpine tundra interface is dominated by pine.

Natural resources in the tree-limit ecotone have been used by man during the past millennium, e.g. haymaking, animal husbandry, lichen harvesting and some selective tree-felling (Kullman 1979; Ljung 2000). In addition, reindeer pastoralism by the Sami population has affected wide areas over the past few centuries. However, early botanical and phytogeographical explorers explicitly state that they found no indications that man had lowered the upper tree-limits (e.g. Kellgren 1893). Likewise, more recent regional studies, based on hundreds of investigated sites, indicate that tree-limit altitudes (above definition) and magnitudes of recent tree-limit shifts do not in general relate to degrees of past human impacts (Kullman 1979; Kjällgren & Kullman 1998). That is not to say, however, that the general structure of the tree-limit ecotone has remained unaltered by direct or indirect human activities.

Methods

Holocene tree-limit evolution

Extensive areas were systematically searched, from the present-day tree-limit and up to the highest mountain peaks, for the presence of preserved megafossil tree remains. The main field-effort was devoted to the highest elevations as the earliest postglacial tree-limit history is likely to be recorded in this vicinity (Kullman & Kjällgren 2000). Particular focus was on small ponds and erosion scars in peat, raw humus and glacial till. In general, these "archives" are physically disturbed or too thin to allow stratigraphical studies. Wood samples were taken to the laboratory for species identification and radiocarbon-dating. In most cases, the species could be ascertained from characteristic wood, bark and branching characteristics. Some ambiguous specimens, however, were determined by Dr. Thomas Bartholin. Where possible, subfossil wood samples were taken close to the pith and the root/trunk junction. In this way, the dates obtained approximate to the time of establishment, despite the possibility that the tree may have lived for some further centuries. Currently, tree-limit pines rarely attain an age of more than 300 years. All samples were closely inspected for possible signs of logging (axe marks) and fire. Radiocarbon-dating was conducted by Beta Analytic Inc., Miami, Florida.

Dates are expressed in the text as conventional radiocarbon years before present (BP), "present" = 1950 AD. Calibrated ages are given in Table 1, according to Stuiver et al. (1998).

Modern tree-limit evolution

The extent of altitudinal tree-limit change over the past century was assessed at sites within the same local drainage areas as those where megafossils were sampled. Thus, present and past tree-limit dynamics are fully compatible with respect to changes in prevailing climatic conditions.

Present-day tree-limits (as defined above) were determined by GPS-measurements (accuracy 1 m) and rounded off to the nearest 5 m. The values obtained were compared with tree-limit positions held in the early-20th century, as deduced from tree age spectra (increment corings) in transects running downhill from the modern tree-limit.

Table 1. Radiocarbon dates from the four study sites.

No.	Lab.no	Site	Species	Radiocarbon age (^{14}C yr BP)	2δ Calibrated range (yr cal. BP)	Midpoint of range (yr cal. BP)	Source
1	Beta-178795	1	Pine	9230 ± 50	10,540–10,240	10,390	This study
2	Beta-172305	1	Pine	9070 ± 70	10,380–10,150	10,265	This study
3	Beta-172317	1	Pine	8500 ± 60	9550–9440	9445	This study
4	Beta-158314	1	Pine	8380 ± 50	9500–9280	9390	This study
5	Beta-169411	1	Pine	8050 ± 70	9120–8660	8890	This study
6	Beta-172316	1	Pine	8040 ± 60	9050–8710	8880	This study
7	Beta-158306	1	Pine	6770 ± 60	7700–7560	7630	This study
8	Beta-169412	1	Pine	6040 ± 60	7010–6730	6870	This study
9	Beta-158308	1	Pine	5930 ± 80	6940–6560	6750	This study
10	Beta-178798	1	Pine	5840 ± 50	6750–6510	6630	This study
11	Beta-179446	1	Pine	4440 ± 70	5310–4850	5080	This study
12	Beta-179447	1	Pine	4360 ± 50	5050–4840	4945	This study
13	Beta-158304	1	Pine	4310 ± 70	5040–4710	4875	This study
14	Beta-180218	1	Pine	3440 ± 70	3870–3490	3680	This study
15	Beta-158307	1	Pine	1590 ± 50	1570–1360	1465	This study
16	Beta-169410	2	Pine	8050 ± 70	9120–8660	8890	This study
17	Beta-173414	2	Pine	7720 ± 80	8630–8380	8505	This study
18	Beta-57644	2	Pine	1190 ± 90	1170–1070	1120	Kullman 2000
19	ST-12023	2	Pine	1155 ± 110	1230–950	1090	Kullman 2000
20	Beta-158305	3	Pine	10,500 ± 60	12,870–11,980	12,425	This study
21	Beta-178794	3	Pine	8190 ± 60	9300–9010	9155	This study
22	Beta-178797	3	Pine	7890 ± 60	8990–8550	8770	This study
23	Beta-178793	3	Pine	6140 ± 100	7260–6750	7005	This study
24	Beta-158302	3	Pine	4680 ± 50	5580–5310	5445	This study
25	Beta-158303	3	Pine	4160 ± 80	4660–4440	4550	This study
26	ST-396	4	Pine	7330 ± 130	8290–7995	8145	Lundqvist 1959
27	ST-397	4	Pine	6840 ± 140	7800–7580	7690	Lundqvist 1959
28	ST-398	4	Pine	6520 ± 170	7560–7330	7745	Lundqvist 1959
29	ST-5747	4	Pine	910 ± 90	975–765	870	Kullman 1980
30	ST-5750	4	Pine	835 ± 90	935–710	825	Kullman 1980
31	Beta-179449	3	Spruce	3970 ± 50	4540–4280	4410	This study
32	Beta-108767	4	Spruce	8490 ± 70	9530–9380	9455	Kullman 2001d
33	Beta-178799	1	Birch	8360 ± 60	9500–9250	9375	This study
34	Beta-179448	1	Birch	4440 ± 70	5310–4850	5080	This study
35	Beta-178796	4	Larch	8160 ± 70	9290–9000	9145	This study
36	Beta-158309	1	Hazel	8670 ± 40	9720–9540	9630	This study
37	Beta-158310	1	Oak	8560 ± 40	9560–9500	9530	This study

These data were collected in the 1970s (Kullman 1979, 1981a, 1986). Updates at the same sites were carried out in 2003 (TL-2003). This approach provides site-specific quantitative data on 20th century positional tree-limit change, i.e. the width of a vertical "advance zone", to be compared with the direction and magnitude of the total range of Holocene tree-limit displacement, as evidenced by the megafossil record. Within the same transects, the positions of the species-limits of birch, pine and spruce, were recorded in the mid-1970s (SL-1975) and in 2003 (SL-2003). This limit is defined as the altitude of the uppermost specimen of a certain tree species, irrespective of size.

On the south-facing slope of Mt. Storvätteshågna (site 1), the present-day age frequency distribution of pine (estimated dates of establishment) was assessed within 20 plots (100 x 100 m) systematically located in a line parallel with the general contours of the slope and separated by 50 m. This sampling comprised the lower part of the advance zone, about 850–860 m a.s.l. All living pines were bored or sawn off (small individuals) as close to the root-stem junction as possible. For larger individuals, i.e. those that were bored, this implies an underestimate of the true age by a few years. Therefore, three years were added to compensate for the growth during the first years. The dates are grouped into age-classes with a width of ten years, which should further alleviate the dating inaccuracy.

The age structure of a sparse population of newly emerged birch saplings was assessed within five 10 x 10 m quadrats on the summit plateau of site 2 (1150 m a.s.l.). The spacing was based on randomly selected coordinates, located by GPS. All individual birch saplings were up-rooted and cut at the lowest point of the stem, which reasonably implies quite accurate dating of germination.

In both the pine and birch "age-subprojects", tree rings were counted in the laboratory under a stereomicroscope.

Results

Holocene tree-limit evolution

A suite of 37 radiocarbon datings of megafossil tree remains forms the core of this study (Tables 1 and 2). Of these, 29 are originally reported here. The dominant species in the total record of dated specimens is pine, with spruce, mountain birch, *Larix sibirica*, *Quercus robur* and *Corylus avellana* as only minor constituents.

Some pine megafossils were unearthed from mineral soil (Table 2). Presumably, the relatively dry, continental climate has enabled long-term preservation by this medium. The majority of samples, however, derive from open scars in thin peat deposits.

From general observations it would appear that the pine remains reported here represent tree-sized specimens, although many were small. There was no evidence of axe-felling. A few pine logs from the past millennium, found slightly above the modern tree-limit, had charred surfaces (Table 2).

The pine dates are distributed from 10,500 to 900 ^{14}C BP (12,400 to 825 cal yr BP), with some gaps discernible, i.e. 7700–6800 ^{14}C yr BP, 5800–4700 ^{14}C yr BP and 3400–1600 ^{14}C yr BP. Plotted against relative altitude, i.e. the tree-limit position in the early-20th century (TL-1915 in Table 3), a clear and conspicuous trend towards gradual and consistent altitudinal tree-limit descent emerges for the entire period 9200 ^{14}C BP (10,400 cal yr BP) and until a century ago. The total regression amounts to 345 m (Fig. 2). Calibration to calendar years does not materially change the general

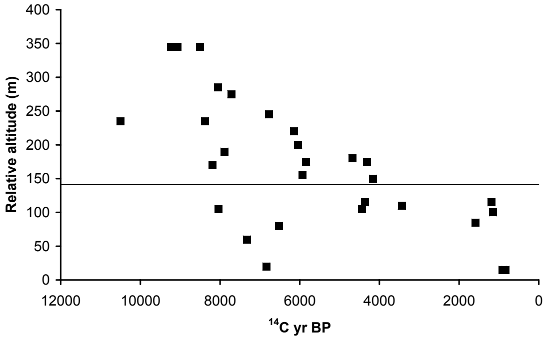

Fig. 2. Radiocarbon dates of megafossil pines, relative to the early-20th century position of the pine tree-limit at the respective site (zero-level). The horizontal line denotes the maximum pine tree-limit advance of 140 m during the past century.

Table 2. Site and sample characteristics of the dates reported in Table 1.

No.	Altitude (m a.s.l.)	Relation to modern tree-limit (m)	Material dated	Setting
1	1180	345	Wood	Peat bank at the shore of a small tarn
2	1180	345	Wood	Exposed by erosion at the shore of a small tarn
3	1180	345	Wood	Peat bank by the shore of a small tarn
4	1070	235	Wood	Small spot with peat mounds
5	1035	285	Wood	Small spot with peat mounds
6	940	105	Wood	Eroding mire
7	1080	245	Wood	Small spot with peat mounds
8	1035	200	Wood	Small spot with peat mounds
9	990	155	Wood	Area with peat hummocks dissected by rivulets
10	1010	175	Wood	Area with peat hummocks dissected by rivulets
11	940	105	Wood	Area with peat hummocks dissected by rivulets
12	950	115	Wood	Area with peat hummocks dissected by rivulets
13	1010	175	Wood	Area with peat hummocks dissected by rivulets
14	945	110	Wood	Transition between mire and morainic hummock
15	920	85	Wood	Exposed in wind-swept heath vegetation
16	1160	285	Wood	Thin peat layer by the shore of a small pool
17	1150	275	Wood	Peat bank by the shore of a small tarn
18	990	115	Wood	Exposed in a sparse birch stand on a steep slope
19	975	100	Wood	Exposed on a steep boulder slope
20	1100	235	Wood	Erosion scar in mineral soil
21	1035	170	Wood	Erosion scar in mineral soil
22	1055	190	Wood	Erosion scar in mineral soil
23	1085	220	Wood	Spot with deep raw humus
24	1045	180	Wood	Thin peat layer
25	1015	150	Wood	Thin peat layer
26	940	60	Wood	"Mire"
27	900	20	Wood	"Mire"
28	915	80	Wood	Thin peat layer
29	910	15	Wood	Exposed in sparse birch forest
30	910	15	Wood (charred)	Exposed in dwarf-shrub heath
31	1000	135	Wood	Raw humus underneath a spruce canopy
32	850	–15	Large cone	Humus deposit in a small lake
33	915	80	Wood	Area with peat hummocks dissected by rivulets
34	920	85	Wood	Area with peat hummocks dissected by rivulets
35	915	40	Twig + 1 cone	Peat erosion scar
36	910	75	Acorn	Peat mound eroded by a rivulet
37	910	75	Nutshell	Peat mound eroded by a rivulet

outlines of the postglacial tree-limit retreat (not shown).

A notable feature (Fig. 3) is that pine was present at high elevations during the final phase of the Lateglacial (Younger Dryas stadial), although dating precision is reduced during this specific interval due to plateux of constant radiocarbon age (Olsson & Possnert 1992). Until ca. 8500 ^{14}C yr BP, pine remains have been recovered exclusively at the highest relative elevations (Fig. 2).

Interestingly, the three uppermost dates derive from a peat bank right at the shore of a small tarn (Sw."Santessons tjärn") just a few meters below the highest peak of the study region (Fig. 4). A reiterated narrative among the local population tells that pine logs could be found at the bottom of this small lake (Forsslund 1919). Stratigraphical investigations by Lundqvist (1951) failed to confirm these stories and it was concluded that pine had never during the postglacial period grown at this eleva-

Fig. 3. Megafossil pine, recently exposed by soil creep and erosion in a boulder slope. Radiocarbon age was 10,500 ± 60 ^{14}C yr BP. Site 3, 1100 m a.s.l. (Photo Leif Kullman, 2002).

tion. Nonetheless, the present study demonstrates that pine was actually present here for at least 1000 years during the earliest part of the Holocene. The remarkable transformation of the mountain landscape during the Holocene is evident also from the finding that by 8000 ^{14}C yr BP pine was growing within the extensive and virtually sterile boulder fields that currently cover the summit plateau at site 2, almost 300 m above TL-1915.

Similar to present-day conditions, megafossil tree birches are sparse. Only two samples from widely different parts of the Holocene were found, viz. ca. 8400 and 4400 ^{14}C BP (Tables 1 and 2). These originate from positions slightly above the present-day tree-limit.

At virtually the same location as that reported for birch, macrofossil remnants of *Quercus robur* (one acorn) and *Corylus avellana* (one nutshell) were recovered within less than 1 m from each other (Fig. 5). Radiocarbon-dating by AMS-technique gave ca. 8600 and 8700 ^{14}C yr, respectively. A characteristic feature of this site at present is the great abundance of snow in winter. Meltwater from the only late-lying snow patch in the area is responsible for active peat erosion, which exposes mega- and macrofossils. Of course, the macrofossils may have been dispersed to this site by birds or wind. However, if not growing at or very close to the sampling site, the probability of deposition at virtually the same spot seems close to zero. Moreover, an early pollen stratigraphical study in a small tarn close to the top of this mountain (see above) suggested that these species actually grew in close proximity to this site at this time (Lundqvist 1951).

Two spruces have been dated within the study area, indicating the presence of this species as early as 8500 ^{14}C yr BP. The youngest date, 4000 ^{14}C yr BP derives from wood fragments preserved quite superficially in the thin raw humus beneath the canopy of a still living tree-sized clonal group (Tables 1 and 2, Fig. 6).

Slightly below the present-day tree-limits, a small twig and a perfectly preserved cone, identified as *Larix sibirica*, were recovered close to the surface of a wind-erosion scar in a thin peat layer (915 m a.s.l.). These remains lay very close to each other and it appears that the cone has been attached to this specific twig. They were radiocarbon-dated as one entity, yielding 8160 ^{14}C year BP (Tables 1 and 2).

Modern tree-limit evolution

During the period 1915–2003, altitudinal tree-limit rise, i.e. TL-2003 minus TL-1915, was established for pine, spruce and birch at each of the four investigated sites (Table 3). The largest shifts, 140 and 135 m, were achieved by pine (Fig. 7) and spruce (Fig. 8), respectively. In contrast to these species, birch has not migrated upslope at some of the investigated sites (1 and 4), although its maximum upward shift at other sites compares with that of pine and spruce (Table 3). Long-term stability of birch distribution in certain settings is further confirmed at sites 1 and 4 as Samuelsson (1914, 1917) and Kellgren (1893) report the uppermost small tree groups at 845 and 875 m a.s.l., respectively, which exactly matches the modern situation. Lack of a positive birch tree-limit response is characteristic of sites that, for topoclimatic reasons (convex relief), display insignificant snow retention into

Fig. 4. Upper: Remnant of a pine tree, excavated from a peat mound right on the shore of a small tarn and dating 9230 ± 50 ^{14}C yr BP. Site 1, 1180 m a.s.l. Lower: The present-day alpine landscape surrounding the megafossil pine depicted in detail above. (Photo Leif Kullman, 2002).

mid- or late-summer (see below). On leeward slopes, with more long-lasting snow cover and moderate-high soil moisture, the birch tree-limit has responded similarly to other species.

To some extent, tree-limit advance by spruce and birch has been accomplished by phenotypical transformation of old-established, climatically suppressed, low-growing krummholz-forms to

Fig. 5. Macrofossil *Quercus robur* (left) and *Corylus avellana* (right), recorded in eroding peat within the present-day tree-limit ecotone. AMS-dating yielded 8560 ± 40 ^{14}C yr BP and 8670 ± 40 ^{14}C yr, respectively. Site 1, 910 m a.s.l. (Photo Leif Kullman, 2002).

Fig. 6. Buried in the raw humus layer underneath the canopy of this layering spruce, pieces of spruce wood were dated 3970 ± 50 ^{14}C yr BP. The main stem died and broke during the cold 1980s and has subsequently been replaced by several secondary, fast-growing sprouts. Site 3, 1000 m a.s.l. (Photo Leif Kullman, 2001).

Table 3. Tree-limit positions at the four study sites in the early-20th and early-21st century, TL-1915 and TL-2003, respectively.

	TL-1915 (m a.s.l.)				TL-2003 (m a.s.l.)				Change 1915–2003 (m)			
Site no.	1	2	3	4	1	2	3	4	1	2	3	4
Pinus sylvestris	835	875	865	875[1]	975	1005	990	975	140	130	125	100
Picea abies	830	975	980	925	900	1060	1115	975	90	85	135	50
Betula pubescens	875	975	905	930	875	1090	1040[2]	930	0	115	55	0

[1] This position was reported as 900 m a.s.l. by Kullman (1981a). Reassessment by GPS in 2003 yielded 875 m a.s.l.

[2] This position is represented by a young tree, that was killed by a minor boulder scree just a few years ago.

Fig. 7. Upper: The position of the pine tree-limit in the early-20th century (TL-1915) is marked by this tree, ca. 160 years old. Site 1, 835 m a.s.l. Lower: At the same locality (altitudinal transect) as above, this pine (975 m a.s.l.), ca. 50 years old, denotes the present tree-limit and a tree-limit rise by 140 m during the past century. (Photo Leif Kullman, 2003).

erect trees. This testifies to climate change as the principal driver. Furthermore, a total lack of pine stumps with axe marks within the advance zone precludes that current tree-limit rise is merely a re-colonization process following ceasing human impact.

Concerning shifts of species-limits, i.e. the leading front of elevational expansion (SL-2003 minus SL-1975), all species moved 25–165 m upwards into the alpine tundra (Table 4). In some cases, the uppermost specimens (e.g. pine at site 3) are large saplings, established some decades ago, that will

Fig. 8. This spruce, which germinated in the late 1930s, represents an uphill tree-limit shift of 135 m over the past 70 years. Site 3, 1115 m a.s.l. (Photo Leif Kullman, 2002).

Table 4. Species-limit positions at the four study sites in 1975 (SL-1975) and 2003 (SL-2003), respectively.

	SL-1975 (m a.s.l.)				SL-2003 (m a.s.l.)				Change 1975–2003 (m)			
Site no.	1	2	3	4	1	2	3	4	1	2	3	4
Pinus sylvestris	965	1015	1070	980	1000	1175	1070	1015	35	160	0	35
Picea abies	915	1060	1115	980	980	1150	1115	1000	65	90	0	20
Betula pubescens	875	1140	920	930	900	1185	980	1010	25	45	60	80

attain tree-size in just a few years, given that current trends of rapid height growth are sustained. In other cases, corresponding individuals are minute and very young seedlings. For example, the birch age structure study (n = 57) at site 2 revealed that all sampled seedlings had germinated during the 1990s and early 2000s. Their height was 12.6 ± 4.5 cm and in 2003 they were just about to overtop the matrix of *Vaccinium myrtillus* and *Nardus stricta*.

Irrespective of species, a majority of the individuals currently making up the advance zone, i.e. between TL-1915 and SL-2003, is strikingly vigorous and has increased rapidly in height during the past decade. This has made pine a much more prominent feature in this landscape. However, some older specimens, spruce in particular, still bear signs of heavy defoliation and branch mortality in response to the cold and ecologically stressing years of the 1980s (cf. Kullman 1997) (Fig. 6). Overall, the recovery from that episode has been remarkable.

A temporal view of the evolution of the pine tree-limit ecotone is provided by the static age structure analysis conducted in the lower part of the advance zone at site 1 (Fig. 9). All currently living individual pines (n = 317) had become established during the course of the 20th and early 21st century. Regeneration "pulses" during some earlier centuries may have occurred, although erect trees were obviously not generated. In this dry, continental and "preservation-friendly" climate at least some stumps or logs from such putative episodes should have been preserved until the present day.

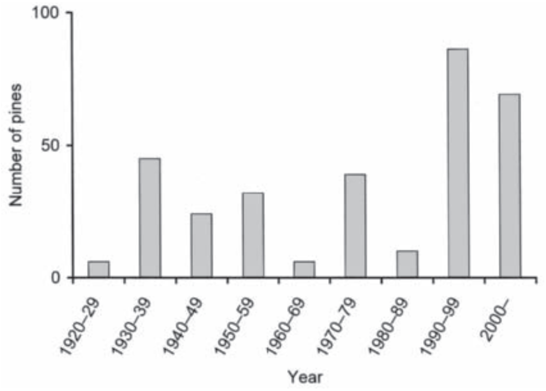

Fig. 9. Composite age frequency distribution in 10-year age classes of pine (all sizes) within 20 quadrats (100 x 100 m), located in the lower part of the advance zone.

The size of the individual age classes differs substantially, indicating a pronounced episodic mode of reproduction/survival. Particularly strong cohorts derive from the 1930s, 1950s, 1970s, 1990s and early 2000s. Pine has consistently become established on the earliest snow-free terrain, in sparse vegetation of dwarf-shrubs and reindeer lichens. Winter observations indicate that establishment of these pine trees has reduced the depth of the local snow cover by canopy interception, i.e. a positive feedback loop implying more favourable conditions for further recruitment. This manifests as distinct sapling clustering in early snow-free spots around these trees.

Practically all pines that germinated prior to the 1970s now comply with the minimum tree definition, i.e. a height of at least 2 m. The age class 1970–79 is highly variable in that respect. Most of the trees in the advance zone have carried large cone crops in recent years. A total of 22 dead saplings (no trees) were found within the plots, which is only ca. 7% of the sampled population.

The landscape level outcome of the reproductional pattern outlined above is the emergence of a sparse belt of pine, ca. 7 trees/ha, that now makes up the tree-limit ecotone almost without admixture of other tree species (Fig. 10). At some other sites, the situation is somewhat more complex, with a tree-limit ecotone composed variably of pine, birch and spruce.

The flora and vegetation in the advance zone have changed conspicuously over the past century. Relative to older landscape descriptions (Kellgren 1893; Samuelsson 1917; Forsslund 1919; Lundqvist 1949), the cover of reindeer lichens (*Cladina* spp., *Cetraria* spp.) has decreased on dry, windy heaths. Summer grazing and trampling by steadily growing reindeer herds seems to be the main reason, although increasing climatic oceanicity may also be involved (Kullman 1997; Öberg 1999). The grass cover (mainly *Deschampsia flexuosa*), e.g. at site 2, has increased dramatically over the past few

Fig. 10. A sparse belt of 4–5 m high pine trees invades the alpine tundra at site 4. (Photo Leif Kullman, 2003).

decades, which may relate to climate warming in conjunction with atmospheric deposition of nitrogen (Kullman 2000, 2003b).

On 30 July 1734, the Swedish naturalist Carl von Linné noticed and described a late-lying snow bank at the base of the S-facing slope of site 4 (Gullander 1980). Even today, large amounts of snow accumulate thereabouts and minor avalanches occur regularly. However, surveillance since the early-1970s has not in any year documented snow remaining after late-June. In 1973, sparse snow bed plant communities (e.g. *Alchemilla alpina*, *Athyrium distentifolium*, *Nardus stricta*, *Polytrichastrum sexangulare*) were recorded in permanent plots established in depressions at this site, 890–920 m a.s.l. A re-survey in 2003, revealed that these communities had virtually vanished, being replaced by luxuriant *Vaccinium myrtillus*, accessory *Vaccinium uliginosum*, *Deschampsia flexuosa*, birch seedlings and common feather mosses. Quite surprisingly, saplings of the exotic *Lupinus polyphyllos* were found in this assemblage (site 4, 890 m a.s.l.). The overall impression, corroborated by comparison of past and present colour photographs, is that the landscape has become greener and lusher over the past 20–30 years.

A few vigorously growing saplings of *Betula pendula*, i.e. the most warmth-demanding *Betula* species in Fennoscandia (Holm 1993), previously unknown in the subalpine belt and above ca. 650 m a.s.l., were recently recorded (site 3) close to the birch tree-limit, 935 m a.s.l. Moreover, exotic tree species, possibly fugitives from fairly distant plantations in this region, have recently appeared at some of the study sites: *Pinus contorta* (0.6 m tall) grows on a mire within the upper and very sparse birch forest belt (site 4, 850 m a.s.l.). *Larix sibirica* (0.2–0.3 m tall) has been found at site 3 (1060 m a.s.l.) and site 4 (960 m a.s.l.), in both cases in the alpine tundra.

Discussion

As outlined in detail below, the present study has virtually reproduced the tree-limit chronology from a more northern site in the Scandes (Kullman & Kjällgren 2000) and all the six points raised in the introduction. These circumstances lend more general credence to these results and inferences and to the methodological approaches used. A main result is that the Holocene tree-limit history does not differ substantially between continental and more oceanic regions of the Swedish Scandes, indicating a major importance of the thermal macroclimate.

Holocene tree-limit evolution (points 1–5)

This study proves the existence of deglaciated mountain summit terrain and presence of trees, > 350 m above modern tree-limits, already by 10,500 ^{14}C yr BP, i.e. shortly prior to the Pleistocene–Holocene transition. Both with respect to deglaciation and tree immigration chronology, this date is substantially earlier than previously inferred (Lundqvist 1951; Huntley & Birks 1983; Fredén 2002), and is also consistent with recent discoveries further north in the Scandes (Kullman & Kjällgren 2000; Kullman 2002a). This implies that plants responded virtually directly to the postglacial warming and invaded the initial periglacial "desert" with striking rapidity and without substantial migrational lag. The latter circumstance suggests the presence of proximal glacial refugia (cf. Kullman 2002a).

Notably, plants (and animals) first immigrated to the highest mountain peaks (nunataks). Since no megafossils have been recovered at relatively low elevations prior to 8500 ^{14}C BP, it is reasonable to infer that these peaks stood out as isolated nunataks until ca. 8500 ^{14}C yr BP surrounded by residual ice bodies and melt water lakes in the valleys. This date is inferred from the first appearance of subfossil pine remnants at relatively low elevations in the mountain landscape (Fig. 2). This mode of deglaciation within this very specific area was suggested on geological evidence, although without absolute dating, by Mannerfelt (1938). Consequently, the subsequent spread of the mountain flora in the landscape has been predominantly downslope as the valley ice gradually disintegrated and vanished.

After attaining its highest position ca. 9200 ^{14}C yr BP, i.e. 350 m above the late-Holocene level, the pine tree-limit has retreated with a virtually constant pace to its lowest position throughout the

Holocene, i.e. in the late-19th century. Thus, the areal extent of alpine tundra was minimal for several millennia during the first part of the Holocene and reached its all-time maximum about a century ago. In this respect, the current results mimic megafossil inferences further north in the Scandes (Kullman & Kjällgren 2000; Kullman 2003a) and at the Eurasian boreal forest–arctic tundra transition (Velichko et al. 1998).

The total Holocene tree-limit recession in the study area is about 150 m smaller than reported by Kullman and Kjällgren (2000) from a region somewhat farther north. Reasonably, this should be understood in terms of the relatively lower mountains in the region concerned here, which were forested and even non-ecotonal for the first millennium or so of the Holocene. This implies that a contemporary cooling-driven tree-limit descent (Kullman & Kjällgren 2000) could not materialize in the study area.

Hypothetically, the scarcity of early-Holocene treeless land, suitable for primary colonization of alpine plants, in conjunction with a poor geological substrate and lack of late-lying snow, has contributed to the floristic poverty of these mountains. Moreover, lack of extensive alpine tundra for several millennia would have precluded the existence of reindeer populations (cf. Barth 1996).

Pine has dominated the retreating tree-limit ecotone throughout the entire Holocene, although scattered birches and spruces seem to have been present for most of the time. Notably, the megafossil record does not indicate the presence of a common subalpine birch forest belt above the pine tree-limit for any period. In contrast with parts of the Scandes with a less continental climate (cf. Kullman 1995), the pine stands have not been replaced by subalpine birch woodlands. In light of modern mountain birch ecology (Kullman 1981b), these circumstances bear witness to the particularly dry summers and poor snow conditions at high elevations during much of the Holocene (see below). There is apparently nothing in the present data to suggest an oceanic climate during the early Holocene, as sometimes argued for northernmost Fennoscandia (e.g. Seppä & Hammarlund 2000).

Contrasting with most pollen-based studies of vegetation history (e.g. Huntley & Birks 1983; Brewer et al. 2002), the present evidence proves an early-Holocene presence of tree species currently absent in the region concerned, i.e. *Larix sibirica*, *Quercus robur* and *Corylus avellana*, right at the modern forest-alpine tundra transitions. *Larix* is currently unknown as native to Fennoscandia, although it grows well, reproduces and spreads when sown or planted, even quite close to the Scandes (see below). *Quercus* and *Corylus*, which are much more thermophilous, have their closest natural occurrences ca. 200 km to the south and 600–700 m lower. A few discoveries of these species as rare macrofossils at high elevations are paralleled by the outcome of similar studies further north in the Scandes (Kullman 1998a, 1998b, 1998c). Adding to this peculiar species composition was spruce, recorded by macro- and megafossils, already by 11,000 ^{14}C yr BP (Kullman 2001d). The existence of these tree species assemblages, without modern analogs, at high mountainous elevations, the so-called "Caledonian forest" appears to be a fairly widespread feature in the Scandes during the early-Holocene. The transformation to a more boreal-like situation was mostly gradual, although the speed increased after ca. 3000 ^{14}C yr BP as the pine tree-limit dropped substantially and spruce expanded regionally in abundance from its old-established sites at high elevations (see below).

Glacio-isostatic land-uplift by ca. 150 m since the early-Holocene (Fredén 2002) explains to some extent the pan-Holocene tree-limit recession by at least 350 m since about 9200 ^{14}C yr BP. Nevertheless, a major residual fraction of 200 m (350 minus 150 m) of the descent is compatible with models of climate evolution (growing season) driven by insolation changes related to variations in the Earth-Sun geometry ("Milankovitch forcing") (COHMAP Members 1988), translating into gradually decreased seasonality, summer cooling and higher humidity. However, the lack of sufficiently high mountain peaks (see above) precludes any tree-limit based assessment in absolute terms, relative to the present, concerning early-Holocene summer temperatures. Further indication for an early postglacial, seasonal insolation pattern substantially different from the present is provided by, although seemingly counter-intuitive, documented tree growth at the highest elevations during the Younger Dryas stadial (cf. Kullman 2002a). Possibly, this was facilitated at certain strictly local leeward sites due to anomalously strong insolation and mild summers. A somewhat analogous situation has been envisaged for southern Greenland (Björck et al. 2002) and parts of Alaska (Elias 2001; Ager 2003).

Regional and even local coexistence of *Larix sibirica*, with continental affinities and thermophilic species such as *Quercus robur* and *Corylus avellana* enhances the impression of a continental, summer warm climate during the early-Holocene. However, the unique species composition cautions against making too precise paleoclimatic inferences, particularly in respect of deviant combinations of seasonal insolation and precipitation patterns. Nonetheless, the coarse, long-term paleoclimatic inferences displayed above are paralleled in widely different parts of the world, which enhances the contention of an ultimate celestial cause (Ritchie et al. 1983; Kremenetski et al. 1998; Horrocks & Ogden 2000; Jensen et al. 2002; Marchal et al. 2002; Makeyev et al. 2003).

The low number of sampled megafossils inhibits any definite conclusions as to the existence of high-frequency tree-limit and climatic variations. Some of the gaps in the long-term record might be artefactual, at least partly, due to inadequate sampling. For example, the trough between ca. 3400 and 1600 ^{14}C yr BP may relate to a relatively small sampling effort in the elevational interval 0–100 m above the late-Holocene tree-limit position. On the other hand, a plethora of paleoclimatic information from other regions of northwestern Europe suggests a severe cooling episode (or episodes) during this period (Neoglacial phase) (Karlén 1976; Gunnarsdóttir 1996; Kullman & Kjällgren 2000; Nesje & Dahl 2000; Hantemirov & Shiyatov 2002; Kullman 2003a). Most likely therefore, the continuous process of climate-driven tree-limit descent accelerated somewhere in this interval, with profound and lasting consequences for the subalpine/alpine landscape (Kullman 2003a). Possibly, this episode was not necessarily triggered by distinct summer cooling beyond the long-term trend. The coeval regional mass expansion of spruce within the mountain taiga of Central-North Sweden (Tallantire 1977) is not readily compatible with a pronounced thermal decline. An ecological threshold relating to increasing effective humidity and snowfall appears more likely as the driving force (cf. Tallantire 1977; Kullman 2001b). Nevertheless, it seems safe to infer that the tree-limit did not exceed a relative level of about 100 m during the period concerned, as interpolated between the closest bracketing dates, i.e. 3400 and 1600 ^{14}C yr BP (Fig. 2).

The gap between 5800 and 4700 ^{14}C yr BP embraces a period of climatically-induced vegetation restructuring as inferred from various sources (Caseldine & Matthews 1987; Kullman 1995; Väliranta et al. 2003).

Lack of high-altitude megafossils in the record between 7700 and 6800 ^{14}C yr BP coincides with a well-recognized episode of glacier expansion and cooling in NW Europe (Klitgaard-Kristensen et al. 1998; Nesje & Dahl 2001). Notably, however, this gap is not particularly distinct in the record by Kullman and Kjällgren (2000), which might suggest that it represents a climatic excursion of very short duration.

Modern tree-limit evolution (point 6)

Long-term cooling and climate stress over much of the Holocene, as outlined above, had brought the tree-limit ecotone into a decadent stage by the onset of the 20th century, with insignificant regeneration and dominance of dead and dying trees in the most marginal populations. Reasonably, this has been the modal situation over much of the Holocene. There are several written (Kellgren 1891, 1893; Forsslund 1919; Lundqvist 1949) and photographic (Fig. 11) accounts of these conditions from the study area. Dendroecological studies further confirm this situation (Kullman 1987, 2001c). In light of the long-term prevalence of this trend in the past and its putative deterministic, celestial mechanism (see above), there would be little (if any) cause to suspect a substantial present-day or near-future reversal (cf. Berger & Loutre 1994). Nevertheless, this is what has actually happened and an anomalous, abrupt and progressive trend break occurred about 100 years ago. A subsequent centennial tree-limit rise by 135–140 m, for all the studied species, matches factual contemporary summer warming by 1.0 ºC (see above), assuming a standard adiabatic lapse rate of –0.6 ºC/100 m. Similar magnitudes of recent tree-limit rise in other parts of the Scandes (Kullman 2001a, 2001c), on the Kola Peninsula of NW Russia (Kremenetski et al. 1999), in Bulgaria (Meshinev et al. 2000) and in western USA (Munroe 2003), support further the contention of global climate warming as the ultimate driving force. This link is evident also at a smaller scale. The age structure analysis within the pine tree-limit advance zone reproduces the result of a similar study at site 2 (Kullman 2000). Both these studies display a distinct episodic pattern, that usually characterizes marginal tree populations limited by heat deficiency (Whipple & Dix 1979; Kullman 1996). The most distinct decadal peaks and troughs coincide with relatively warm and cold periods, respectively, according to Alexandersson (2002). This course of demographic evolution translates into a new biogeographic pattern, i.e. a sparse belt of pine trees, above existing patches of subalpine birch forest, and invading the alpine tundra. It may be hypothesized that this process will accelerate in a positive feedback loop in the future, as the first wave of trees modifies and improves the local environment and facilitates further establishment and growth. This seems to be a more general mechanism for tree-limit maintenance and patterning (e.g. Germino et al. 2002; Alftine & Malanson 2004).

Also the general species-limit advance during the past few decades coincides with documented warming, and is paralleled in other parts of Fennoscandia (Luoto & Seppälä 2000; Molau & Larsson 2000; Kullman 2002b, 2003b).

The interspecific discrepancies in recent response patterns may have a bearing on the future evolution of the tree-limit ecotone. The inability of mountain birch, contrasting particularly with pine, to expand in altitude in dry and snow-poor environments is a well-established fact also in other parts of the Scandes (Kullman 1979, 1981a). This circumstance raises some doubt as to the long-term predominance of a discrete subalpine birch belt, wherever it exists today, in a future situation of sustained global warming and with reduced amounts of late-lying snow at high elevations. In such a scenario, pine, a decidedly invasive species at high-altitude and nutrient-poor sites (Richardson & Bond 1991), appears to be particularly successful. The sparse heath birch woodlands in continental regions of Fennoscandia would be suited for transformation to montane pine woodlands. However, if the current trends towards increasing climatic oceanicity proceed much further, the situation would become more complex (Crawford et al. 2003).

Fig. 11. Until about a century ago, and for most of the preceding Holocene, the pine tree-limit ecotone has had the character of a veritable "graveyard" for the victims of more or less steady tree-limit recession. Site 1, ca. 900 m a.s.l. (Photo Karl-Erik Forsslund, 1912. Reproduced by permission of Dalarnas Museum, Falun).

The present results demonstrate that certain cold-marginal tree vegetation responds to climatic change over a period of less than 100 years (cf. Kullman 1997, 2002b, 2003b). This insight thwarts some sceptical generalizations in that respect (Kupfer & Cairns 1996), but agrees with other paleoecological and neoecological records (cf. Williams et al. 2002; Post 2003). All available evidence suggests that the tree-limit for most of the Holocene has been in a dynamic equilibrium with climate, a situation that may prevail in the future. The realism of model forecasts of rapid and substantial tree-limit advance in the near future in response to sustained global warming (e.g. Peters & Darling 1985; Kellomäki et al. 1997) is, in principle, supported by this empirical study. However, upward shifts will certainly not occur everywhere in the alpine landscape and at the same pace. This relates to the fact that the tree-limit position is controlled by complex interactions of climatic, topographic and biological factors, the relative strength of which varies within the heterogeneous mountain landscape (cf. Kullman 1979; Kjällgren & Kullman 1998; Payette et al. 2001). Moreover, a warmer but increasingly oceanic climate may counteract tree-limit advance in certain maritime regions (cf. Crawford et al. 2003), although not initially in a region with a continental climate.

Major aspects of the ground cover evolution during the past century, i.e. grass expansion, decline of snow bed vegetation and invasion of exotic plant species, agree with more theoretical predictions concerning vegetation responses to future climate warming, although the mechanisms may be complex (Crawford 1997; Dukes & Mooney 1999; Despain 2001). Vanishing or profoundly changing snow bed vegetation is reported also from other regions of Europe (Grabherr 2003; Virtanen et al. 2003; Kullman 2004a), which underpins fears that this type of alpine vegetation is particularly endangered in a future warmer world (IPCC 2001b).

Matching maximum 20th century tree-limit rise (140 m) with the entire Holocene pine tree-limit chronology (Fig. 2) suggests a tentative interpretation that the former process represents the largest and most rapid warming over at least the past 4000 radiocarbon years in the study region. When the relative altitudes in the chronology are adjusted for glacio-isostatic land uplift, i.e. ca. 100 m over the past 7000 years (Fredén 2002), it appears that modern tree-limits and associated summer temperatures are anomalous in context of the past 7000 radiocarbon years. This inference is consistent with more extensive megafossil data sets from similar studies farther north in the Scandes (Kullman & Kjällgren 2000; Kullman 2003a). Also in other parts of the world, an increasing body of paleoclimatic records have provided broadly similar paleoclimatic inferences as those in the present study (e.g. Douglas et al 1994; D'Arrigo et al. 1996; Haeberli & Beniston 1998; Luckman & Kavanagh 2000; Thompson 2000; Mann & Jones 2003; Perren et al. 2003). Thus, 20th century warming and associated biological consequences in the study area fit an extra-regional pattern that is beyond the range of expected late-Holocene natural variability in the study region. Definite conclusions in this respect have to await an even more extensive megafossil record.

ACKNOWLEDGEMENTS

Financial support for this study was provided by the Swedish Research Council. I am most grateful to Robert M. M. Crawford, Lena Kjällgren and an anonymous reviewer for valuable comments on the manuscript and to Hans Alexandersson (Swedish Meteorological and Hydrological Institute) for providing unpublished meteorological data.

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