

# Pine (*Pinus sylvestris*) treeline dynamics during the past millennium — a population study in west-central Sweden

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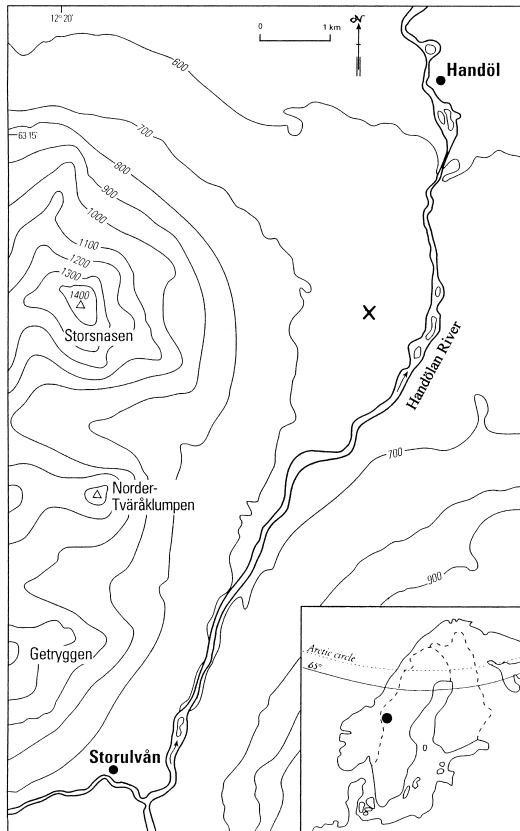
Dynamics of a pristine and fire-free treeline population of Scots pine (*Pinus sylvestris*) over the past millennium was reconstructed at a site in the southern Swedish Scandes. At the broadest temporal scale, population change was analysed from radiocarbon-dated megafossil wood remains (stumps, trunks, etc.) lying on the ground surface. Recent stand history was derived from age structure analysis and repeated photography of the living pine population. The study population has undergone gradual and total demise (deforestation) between the 11th and 19th centuries AD, implying a transformation from a sparse forest structure to near tundra conditions. Pine establishment in the past 50 years has increased tree density to levels that might have existed more than 1000 years ago. The inferred course of pine population change broadly concurred with local, regional and hemispheric paleoclimatic proxies and paleotimeline histories, as well as instrumental temperature records. Little establishment occurred during the cold conditions of the Little Ice Age, while pine recruitment in the latter half of the 20th century was inferred to be exceptional in the context of at least the past one thousand years.

Key words: age structure, climate change, “global warming”, Little Ice Age, megafossils, millennial-centennial scale, *Pinus sylvestris*, Swedish Scandes, treeline

## Introduction

Expected global warming in the near future is anticipated to affect biota and biogeographical patterns in ways that can be only imagined from ecological models founded on empirical trends of sufficient length (cf. Grabherr *et al.* 2001). Mountain ecosystems in particular, with most of the component species growing at the extreme limit of climatic tolerances, are characterized by an inherent sensitivity to climate change (Boer *et al.* 1990, Holten & Carey 1992). Accord-

ingly, various studies of high-altitude treelines demonstrate that 20th century climate warming has caused an increase in treeline elevation (Hustich 1958, LaMarche 1973, Kullman 1979). This study focused on the alpine treeline of Scots pine (*Pinus sylvestris*) in the southern Swedish Scandes. Treeline is the ecotonal gradation between closed boreal forest and the uppermost, solitary tree-sized (at least 2 m tall) pines, i.e. the tree-limit. The treeline ecotone is a most useful paleoclimatic indicator, and treeline ecology has emerged as one of the fundamentals on which pre-



**Fig. 1.** Location map showing the study site (x) in Handölan Valley (contour interval 100 m). The current treeline of *Pinus sylvestris* runs at the 700-m contour.

dictive global change ecology develops (Peterson 1998, Holtmeier 2000, Kullman 2001a). Empirical effect studies demonstrate that alpine treelines respond even to the relatively small climatic shift that characterizes the past century, by changes in structure and elevation (Kullman 1979, 2001a, Kremenetski *et al.* 1999, Meshinev *et al.* 2000, Juntunen *et al.* 2003, Moiseev & Shiyatov 2003, Munroe 2003, Penuelas & Boada 2003).

Data on the timing and magnitude of tree establishment and survival in the past offer further insights into the potential responses of treelines in an anticipated warmer world. Several such studies have been carried out with different analytical approaches and temporal resolution (e.g. LaMarche 1973, Wick & Tinner 1997, Kremenetski *et al.* 1998, Eronen *et al.* 1999, Kullman & Kjällgren 2000, Kullman 2001b, 2004a, Payette *et al.* 2002, Ali *et al.* 2003). Few

population-level studies of alpine treelines, however, bridge the gap between the early and the late Holocene (but *see* LaMarche 1973).

This study was located in an area where detailed treeline histories (megafossils) are thoroughly reconstructed since the Late-Glacial (Kullman & Kjällgren 2000, Kullman 2001b, 2004a) and over the past century (Kullman 1997, 2001a). Accordingly, pine is the dominant tree within the treeline ecotone during the early Holocene, prior to about 7000 cal. BP. Tree-limits of *Pinus sylvestris*, *Picea abies* and *Betula pubescens* ssp. *tortuosa* are then positioned more than 500 m above their current positions, as a consequence of the postglacial summer thermal optimum, i.e. 11 000 to 10 000 cal. BP (Kullman & Kjällgren 2000, Kullman 2001b, 2004a). Gradual cooling (centennial to millennial scale) by 2–3 °C (corrected for land-uplift), until about a century ago, forces decline in upper pine forest density and treeline elevation to Holocene record lows. Over the past century, this regressive trend reverses as summer temperatures in the Scandes and most of central and northern Sweden increase by about 1 °C in a two-step process, 1915 to 1940 and 1990 to the present (Alexandersson 2002, Kullman 2004c). This course of climate change is broadly substantiated by glacier recession and permafrost reduction in the study region (Lundqvist 1969, Kullman 2003). In response, a profound transformation in the ecological landscape appears to be underway in this region as previously moribund and sparse pine stands are growing denser and more vital, while tree-limits of *Pinus*, *Picea* and *Betula* shift 150–160 m upslope (Kullman 2001a, 2004b). The temporal resolution of existing treeline chronologies (*see above*) are poor during the late Holocene. Against this background, the purpose of this paper was to reconstruct pine treeline history for the past 1000 years.

## Study area

The study was carried out at the mouth of Handölan Valley in the southern Swedish Scandes, province of Jämtland (Fig. 1). The pine stand chosen for detailed study was located on the lower, east-facing slope of Mt. Storsnasen,



**Fig. 2.** View from the west over the sampled pine population. Macrofossil pine remnants are indicated by the inflated plastic bags. Some samples are hidden among and behind the trees. Photo: 11 June 2003.

670 m a.s.l., 63°14.023'N, 12°25.896'E (Fig. 1). The bedrock is made up of Svea amphibolites and covered with glaciofluvial deposits and peat of variable thickness. The elevation of the valley floor ranges between 650 and 700 m a.s.l., and surrounding mountain peaks reach 1100–1400 m a.s.l. The nearest meteorological station is Storlien/Visjövalen at 642 m a.s.l., about 19 km northwest. Mean temperatures (1961–1990) for January, July and the year are  $-7.6$ ,  $10.7$  and  $1.1$  °C, respectively. Total annual precipitation averages 847 mm for the same period. Deglaciation of the valley bottom took place about 9500 cal. BP, while the highest peaks had been free of ice and stood out as nunataks about 14 000 cal. BP (Kullman & Kjällgren 2000).

The landscape is a mosaic of extensive mires, almost treeless, windswept heaths, mountain birch woodlands and small, isolated stands of pine and spruce. Preferentially, pine grows on minor, south-facing slopes of the local topography, clearly indicating the marginal character of its distribution hereabouts.

The tree cover within the study plot consists of mostly young trees and saplings, a few living mature trees, but no standing snags. Except for one charred log, probably caused by a lightning fire, no evidence of forest fire or other major disturbance could be discerned. The past and present tree covers appear virtually untouched by human activity, although there is a long history (300–400 years) of grazing and trampling by semi-domestic

reindeer in the region. The western third of the plot is most exposed and pine cover is sparse. Active cryoturbation, resulting in open frost boils and low mounds, characterizes this portion of the plot. *Calluna vulgaris* dominates the patchy and open ground layer, with associated species such as *Empetrum hermaphroditum*, *Betula nana*, *Carex bigelowii*, *Arctostaphylos alpina* and *Loiseleuria procumbens*. In addition, reindeer lichens (*Cladina* spp.) grow in the gaps among the dwarf shrubs. The remaining two-thirds of the plot is more sheltered, with more closed tree and ground cover. A few tiny birch trees occur throughout the stand. The forest floor displays a typical boreal forest structure and composition; the dominants include *Calluna vulgaris*, *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*. A well-developed ground cover of common “feather mosses” (*Hylocomium splendens*, *Pleurozium schreberi*) is present in this part of the plot.

## Methods

Field sampling was carried out in a plot (90 × 30 m, oriented east to west) embracing an entire treeline population of pine that occupies a well-drained outcrop of glacial lake sediment, surrounded by a virtually treeless mire (Fig. 2). Based on regional-scale reconnaissance surveys, the stand was selected as typical for the appearance of pine in the treeline ecotone.



**Fig. 3.** The death of the oldest megafossil pine recovered in the sample plot was dated to the 10th century AD. Photo: 12 June 2003.

The sample plot was systematically scrutinized for the presence of subfossil pine remnants. Minor mounds and elongated rises were probed

by digging, which has reasonably uncovered the vast majority of preserved pines. All dead pine remnants (stumps and logs) recovered at the

**Table 1.** Radiocarbon dates of megafossil pines within the sample plot.

No.	Lab. no.	Radiocarbon age ( $^{14}\text{C}$ BP)	$2\sigma$ Calibrated range (cal. AD)	Material dated
1	Beta-180217	$1080 \pm 70$	790–1040	Large stump
2	Beta-180193	$870 \pm 60$	1020–1270	Slender trunk
3	Beta-180201	$650 \pm 60$	1270–1420	Slender trunk
4	Beta-180198	$630 \pm 30$	1290–1400	Wood in a mound
5	Beta-180216	$620 \pm 60$	1280–1420	Wood in a mound
6	Beta-180204	$590 \pm 60$	1290–1430	Large stump
7	Beta-180205	$550 \pm 60$	1300–1450	Trunk remnants
8	Beta-180203	$510 \pm 30$	1400–1440	Large stump
9	Beta-180192	$460 \pm 70$	1320–1630	Wood in a mound
10	Beta-180214	$430 \pm 50$	1420–1630	Wood in a mound
11	Beta-180200	$390 \pm 40$	1430–1630	Medium-sized trunk
12	Beta-180195	$360 \pm 50$	1440–1650	Basal part of a trunk
13	Beta-180211	$350 \pm 60$	1430–1660	Wood in a mound
14	Beta-180215	$320 \pm 60$	1440–1670	Wood in a mound
15	Beta-180213	$310 \pm 60$	1450–1670	Wood in a mound
16	Beta-180210	$310 \pm 50$	1460–1660	Slender trunk
17	Beta-180212	$290 \pm 60$	1460–1680	Wood in a mound
18	Beta-180191	$280 \pm 60$	1460–1680	Slender trunk
19	Beta-180206	$250 \pm 60$	1490–1690	Medium-sized trunk
20	Beta-180207	$250 \pm 60$	1490–1690	Basal part of a trunk
21	Beta-180196	$250 \pm 50$	1510–1680	Medium-sized trunk
22	Beta-180208	$220 \pm 70$	1640–1680	Wood in a mound
23	Beta-180202	$180 \pm 60$	1650–1800	Wood in a mound
24	Beta-180197	$180 \pm 40$	1650–1800	Wood in a mound
25	Beta-180190	$180 \pm 50$	1650–1800	Wood in a mound
26	Beta-180194	$180 \pm 40$	1650–1800	Medium-sized trunk
27	Beta-180209	$150 \pm 60$	1680–1810	Basal part of a trunk



soil surface, or partly buried, were radiocarbon-dated. Species were determined using remaining bark fragments on the trunks. Dating comprised the outer section of the stem and should roughly indicate the death of a tree, although an unknown proportion of the youngest wood may have been eroded or decomposed, and typically, the inner rings were lost to heartrot. In most cases, patches of bark remained at the stem surface and sampling of wood for dating concentrated on these parts. Thus, dating inaccuracy due to missing outer rings should not be overstated. Recovered specimens were closely inspected for signs of logging or fire. Many were in too decayed a condition to allow dendrochronological dating or building of lengthy ring-width chronologies, based on a sufficiently large sample. Unfortunately, radiometric dating is seriously inaccurate after about AD 1650 due to fluctuations in the atmospheric  $^{14}\text{C}$  level (Stuiver & Pearson 1986). During this period, there were several possible calendar ages for any given radiocarbon date. This methodological caveat prevented any detailed temporal interpretation of the age data.

Radiocarbon dating was conducted by Beta-Analytic Inc. Dates were converted to calibrated age (cal. AD) according to Stuiver *et al.* (1998). For the sake of simplicity, mid-point values within  $2\delta$  calibrated range were given.

All living pine seedlings, saplings and trees in the study plot were sampled. The ages of pines shorter than 2 m were determined from branch whorls and terminal bud scars. Individuals taller than 2 m were cored to the pith, 10–15 cm above the root collar and ring counting was made under a stereomicroscope. Based on aging of true root-collar sections from a small subsample ( $n = 10$ ) of pines ranging between about 100 and 5 years, 5 and 2 years were added to the original estimate of each individual within the largest and smallest size-class, respectively (cf. Stöcklin & Körner 1999). These dates were grouped into 10-year age classes, which should further alleviate any problems with dating inaccuracy.

## Results

Altogether 27 subfossil remnants from mature pine trees were localized within the sample plot

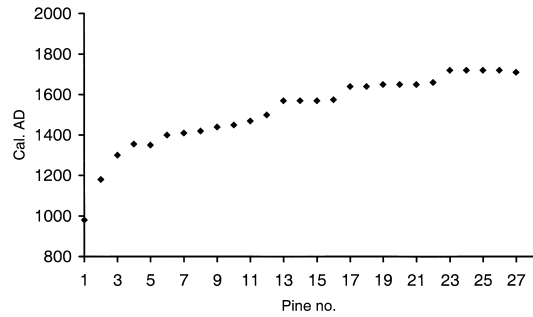


Fig. 4. Approximate death dates of all recovered pine megafossils.

(Fig. 3). Given the thorough and systematic scrutiny of the small sample plot, the potential for long-term preservation (1500 years at least) of subfossil pine wood in open, well-drained treeline settings (Bartholin & Karlén 1983), and the presence of slender (10–15 cm in diameter) and relatively old specimens, it seems unlikely that any trees were missed by the survey. Two stems (nos. 19 and 21) with a basal diameter of about 25 cm, displayed incomplete (due to rot) ring counts of 450 to 500 years.

Radiocarbon dating yielded approximate death dates that extended about 1000 years back in time (Table 1). As mentioned above, dating and calibration accuracy is poor after AD 1650. With this reservation, it appears from Fig. 4 that the recovered subfossil pine population died out gradually over the past millennium, although mortality was relatively insignificant prior to about 1300 AD. No tree remnants were dated after about AD 1800 and, thus, depletion of mature pines from the studied population was largely a pre-19th century process. The age structure analysis of living pines (Fig. 5) indicated that the virtually treeless state remained for most of the 19th century. However, some seedling regeneration occurred over this period, although it may be inferred that just two pines had grown to tree size by the end of the century. Coring at different stem heights of those few specimens that became established during the 19th century showed that it took at least 50–75 years to attain the height of 2 m. Multiple branching at the stem bases indicated that they suffered from repeated top dieback in an open, windswept and snow-poor environment (Fig. 6). Nevertheless,

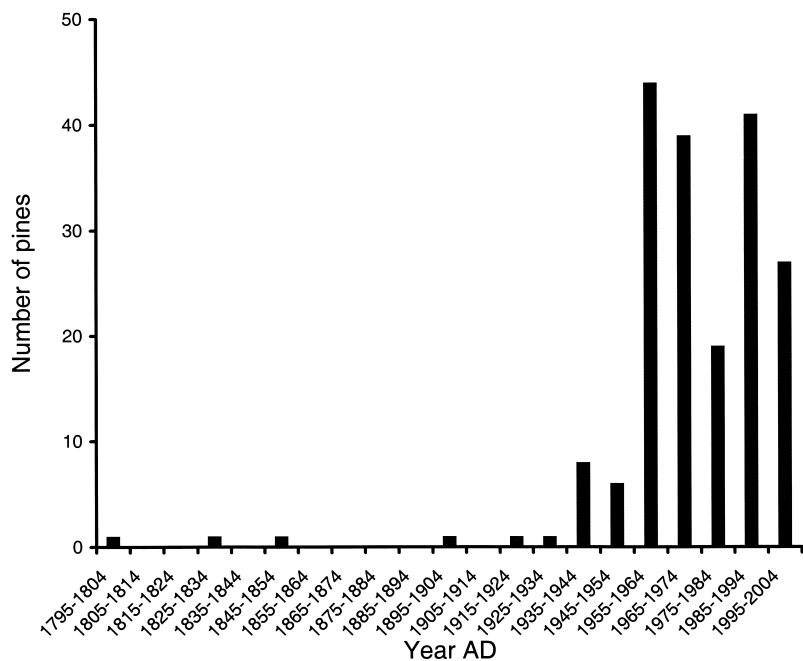


Fig. 5. Age structure (10-yr classes) of the entire living pine population within the sample plot ( $n = 187$ ).

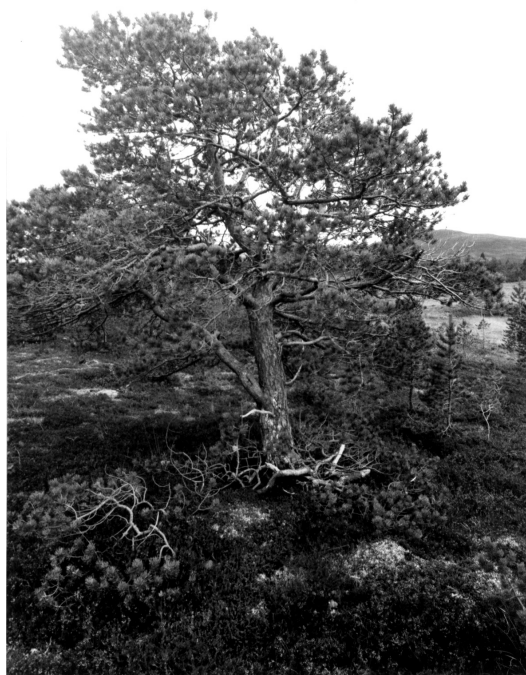


Fig. 6. The oldest living pine germinated in the late-18th century in an open and tundra-like environment. Multiple basal branches indicate that it suffered repeated dieback until it reached tree-size after about 75 years.

by the early 20th century few pines had reached a size that usually implies reproductive maturity. Centred around these trees, a distinct pulse of regeneration commenced during the 1930s, and has, with some variable success, continued to the present. As a consequence, an open woodland structure has replaced former tundra conditions (Fig. 7), except in the westernmost part of the plot, which still has a near-tundra character. This recent increase in regeneration was initiated in the least exposed (easternmost) part of the plot and has proceeded against a spatial gradient of increasing harshness; wind exposure in combination with somewhat increasingly convex terrain. Prevailing winds in the study area are from W to SW and may be locally very destructive to the tree- and ground cover (Kullman 2005). Annual observations indicated rapid height growth and virtual absence of winter needle injuries (browning) during the past 10–15 years among the pines originating from the past 50 years. A process of conspicuous infilling since the mid-1980s was clearly discernible from repeat photography (Fig. 8). Notably, scattered young trees and saplings are spreading out into previously treeless mires surrounding the sample plot.

**Fig. 7.** The large pine became established in the 1920s and has subsequently grown substantially in size. This might be the source of seed of surrounding young pines, originating from the 1950s and onwards. Photo: 14 January 2004.



## Discussion

The initial part of the present treeline chronology, i.e. around AD 1000, fell within the so-called Medieval Warm Period (Lamb 1982, Hughes & Diaz 1994, Esper *et al.* 2002), when treelines and their driving temperatures in north-western Europe were substantially higher than during the late 19th century (e.g. Hiller *et al.* 2001, Kullman 2003, Hammarlund *et al.* 2004, Kremenetski *et al.* 2004). Given that pine may live for at least 700–800 years (Sirén 1961, Engelmark & Hofgaard 1985), it can be inferred that a large proportion of the subfossil pines that died during the past millennium originated from a phase of relatively favourable climatic conditions during the Medieval period. Whether the current stand density and stature exceeded that of the Medieval optimum cannot be judged by the data presented here.

A long-term and steady decline of the treeline population occurred between AD 1000 and 1800. This observation agreed with evidence from other studies in the region (Kullman 1986, 1987a, 1987b, 2000). Likewise, pollen data from nearby sites (Segerström & von Stedingk 2003, Hammarlund *et al.* 2004) indicate continuous cooling, a gradual reduction in pine forest cover and a landscape change finally leading to treeless, near tundra conditions over approximately the past 900 years. Of course, it is possible that short-term climatically favourable episodes

existed during this long period as some of the subfossil pine samples in this study likely germinated during this interval. Although rare, pine trees older than 300 years exist in somewhat more sheltered localities (minor south-facing slopes) in the valley landscape outside the study plot. In such situations, long-term population decline was less complete and post-Little Ice Age reforestation was initiated earlier than in the relatively more exposed study plot (Kullman 1986, L. Kullman unpubl. data).

Almost a century ago, and in line with evidence presented above, botanists reported dead and dying pine forests in the Handölan Valley (review in Kullman 1986) and in treeline landscapes in Norway and Finland (Olafsen 1911, Nordhagen 1923, Kranck 1909). Accordingly, a 1914 photo shows a stand of dead pine stems close to the study site (Fig. 9).

The local, millennial-scale treeline decline outlined in this study fits well the youngest phase of the regional treeline history, showing consistent retraction to the lowest Holocene position, during the late 19th century (Kullman & Kjällgren 2000). This process was inferred to be conditioned ultimately by a gradual decrease in summer insolation (Milankovitch mechanism), which caused gradually cooler summers. During the period 500 to 100 years ago, the so-called Little Ice Age, temperatures appear to have reached their all-time Holocene low (Grove 1988, Bradley & Jones 1993). The association





**Fig. 8.** — **A:** Mature pine that germinated in the 1830s and attained tree stature by the early-20th century. Photo: 16 March 1983. — **B:** Over the past two decades, the young pine saplings have grown substantially in size and the local landscape has changed fundamentally. Photo: 14 March 2004.

of the treeline decline of the past 1000 years with this episode was indicated from the fact that mortality appeared to have been relatively low prior to about AD 1400, i.e. the onset of the Little Ice Age in the southern Scandes (Nesje *et al.* 1991).

Despite a small and geographically limited study, the outlined history of treeline dynam-

ics in the Handölan Valley, both its subfossil and living phase, compares well with reconstructed thermal history of the northern hemisphere (Mann & Jones 2003) and concurs with treeline dynamics in Siberia and North America (LaMarche 1973, MacDonald *et al.* 1998b, Moiseev & Shiyatov 2003, Munroe 2003). However, the record of continuous population decline prior to the 20th century was not entirely compatible with a reconstructed low-frequency temperature record based on tree-ring widths of “bog pines” from a near-treeline site 50 km east of the study area (Gunnarson & Linderholm 2002). That study did not indicate the same consistent cooling trend over the past millennium prior to about AD 1900, as may be inferred by the present data. On the contrary, a clearly positive trend emerged from the mid-17th century until around AD 1950, whereafter the trend is distinctly negative. Since that dendroclimatological reconstruction fails to account adequately for the instrumentally recorded temperature variations during the 20th century, its validity for earlier periods should not be taken for granted (cf. Eronen *et al.* 2002).

The continuous infilling process (population expansion) since the early 20th century and particularly during the past 50 years of fluctuating temperatures (Kullman 1997, Alexandersson 2002) might suggest that summer temperature-dependent seed viability (Henttonen *et al.* 1986) is not entirely limiting for pine treeline population dynamics and some viable seed may be produced also during relatively cold periods (cf. Juntunen *et al.* 2002). Conditions for survival and growth of seedlings and saplings might be of equal or greater importance, particularly during winter and spring (Payette & Lavoie 1994, Kullman 1997, MacDonald *et al.* 1998b). Evidence for the possibility of rapid, cold-induced premature, stand-level dieback and mortality of full-sized treeline pines as well as seedlings and saplings is documented in some investigations within the study area during particularly cold episodes of the late 20th century (review by Kullman 1997). These empirical studies demonstrate that pine populations at the treeline are vulnerable even to short sequences of exceptionally cold winters, mainly as a consequence of deep and persistent soil freezing causing winter/spring needle and bud desiccation. Hypotheti-





**Fig. 9.** — **A:** Historical photograph (12 July 1914, photo: Harry Smith) showing abundant dead trees. — **B:** Present (19 July 2002), a prospering new pine generation dominates this view (Kullman 1986). This site is about 0.5 km south of the study site and at the same altitude.

cally, these circumstances imply that treeline decline during the past millennium was largely a question of increased mortality.

To some extent, the pulse of recruitment since the 1950s may represent a positive feedback process. It may be that the increasing stand density influences e.g. snow and wind conditions in a way that promotes seedling establishment, growth and survival (cf. MacDonald *et al.* 1998a). Mechanisms of this kind are suggested to be of great importance for the maintenance and patterning of alpine treelines (e.g. Alftine & Malanson 2004). Substantial densification in treeline populations seems to be a common phenomenon

in northern and high-elevation environments, and is obviously more frequently occurring than actual elevational treeline advance (Payette & Filion 1985, Scott *et al.* 1987, MacDonald *et al.* 1998a, 1998b, Veijola 1998, Stöcklin & Körner 1999, Juntunen *et al.* 2002).

Treeline progression in the 20th century changed the character of the landscape into a stage that seems to be exceptional with respect to density of tree sized pines for at least the past 1000 years. This development coincided with climate warming by a modest 1 °C in the study region (Kullman 2001a, 2004c, Alexandersson 2002), which suggested a causal relationship.

If future climate change concurs with model projections, e.g. a mid-range scenario of warming by about 3 °C (IPCC 2001, Räisänen *et al.* 2004), even more far-reaching transformation and diminuation of the alpine landscape would occur (Kullman 2004b). This means that we would be facing a situation whose closest analogue can be gleaned during the early-Holocene thermal optimum, when treelines in the Scandes reached 500–600 m higher uphill than a century ago (Kullman & Kjällgren 2000, Kullman 2004a).

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