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Climatically induced regeneration patterns of marginal populations of *Pinus sylvestris* in northern Sweden

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Abstract. The age-structure of Scots pine (*Pinus sylvestris* L.) was analysed in climatically marginal populations in northernmost Sweden. The regeneration pattern (1450-1990 A.D.) was clearly episodic in character. Distinct peaks were evident for the periods 1540-1569, 1650-1659, 1750-1789, 1820-1839, 1870-1879, 1920-1959 and 1970-1979. Regeneration gaps occurred for the periods 1570-1649, 1660-1749, 1790-1819, 1840-1849, 1880-1919 and 1980-1989. Peaks and troughs were in good variance with warmings and coolings, respectively, inferred in a previous dendrochronological analysis of pine in the same region (Briffa *et al.* in press). On this basis it is suggested that in the absence of major disturbance regeneration dynamics of pine in marginal habitats is foremost a function of summer temperature, rather than autogenic stand dynamics.

Key-words: Age-structure, marginal populations, climatic variability, *Pinus sylvestris*, North Sweden

Introduction

Plant population structure at northern or elevational margins of distribution is generally assumed to reflect past thermal (summer) variability (Bujtenen and Stern 1967; Wein and El-Bayoumi 1983; Davis 1986; Brubaker 1986). Possibly, major disturbance and autogenic population processes might also be influential (cf. Stewart and Rose 1989; Ågren and Zackrisson 1990). In the southern Swedish Scandes, Scots pine (*Pinus sylvestris* L.) has responded to the warming of the first half of the 20th century with altitudinal advance and infilling of marginal populations (Kullman 1990, 1991a). Analogous responses have been reported for cold marginal tree populations elsewhere in the northern hemisphere (Hustich 1958; LaMarche 1973; Payette and Filion 1985; Scott, Hansell and Fayle 1987). However, plant-climate relationships close to the tree-limit have rarely been analysed in a more long-term perspective due to the lack of long climatic time series. Such independent reconstruction of the climatic background would make it possible to separate structural effects of autogenic stand dynamics or major disturbance from directly climatically induced ones.

The present study analyses the age structure of natural mixed pine-birch populations, only slightly below the altitudinal pine tree-limit (i.e. stems with a minimum height of 2 m) in northernmost Sweden. The results are discussed against the background of a dendrochronological reconstruction (pine) correlating to the April-August temperature (ring width) from the same region and covering the period 700-1989 A.D. (Briffa *et al.* in press). By matching peaks and troughs of the pine age structure with these proxy climate data, the hypothesis of climatic regulation of marginal pine regeneration dynamics can be adequately tested.

Study area

General overview

The study focuses the transition between coniferous boreal forest and subalpine/subarctic birch forest in northernmost Sweden, approx. 68°20' N, 20°10'E (Fig. 1). Sample plots were analysed along a NE-SW line transect (*c.* 20 km) between the hamlet Idivuoma and Mt. Kuormakka. The elevation ranged between 425 and 450 m a.s.l., which is about 50 m below the pine tree-limit. The tree-limit of birch is at *c.* 650 m a.s.l.

The climate has a local continental character, i.e. relatively cold winters, warm summers and a sparse snow cover. The area is at the fringe of the zone of discontinuous permafrost (Rapp 1982). The bedrock is mostly syenite and basaltic greenstones. More details of the setting are provided by Kullman and Engelmark (1991).

Regeneration

The investigated woodlands are made up of sparse populations of polycormous birch (*Betula pubescens*

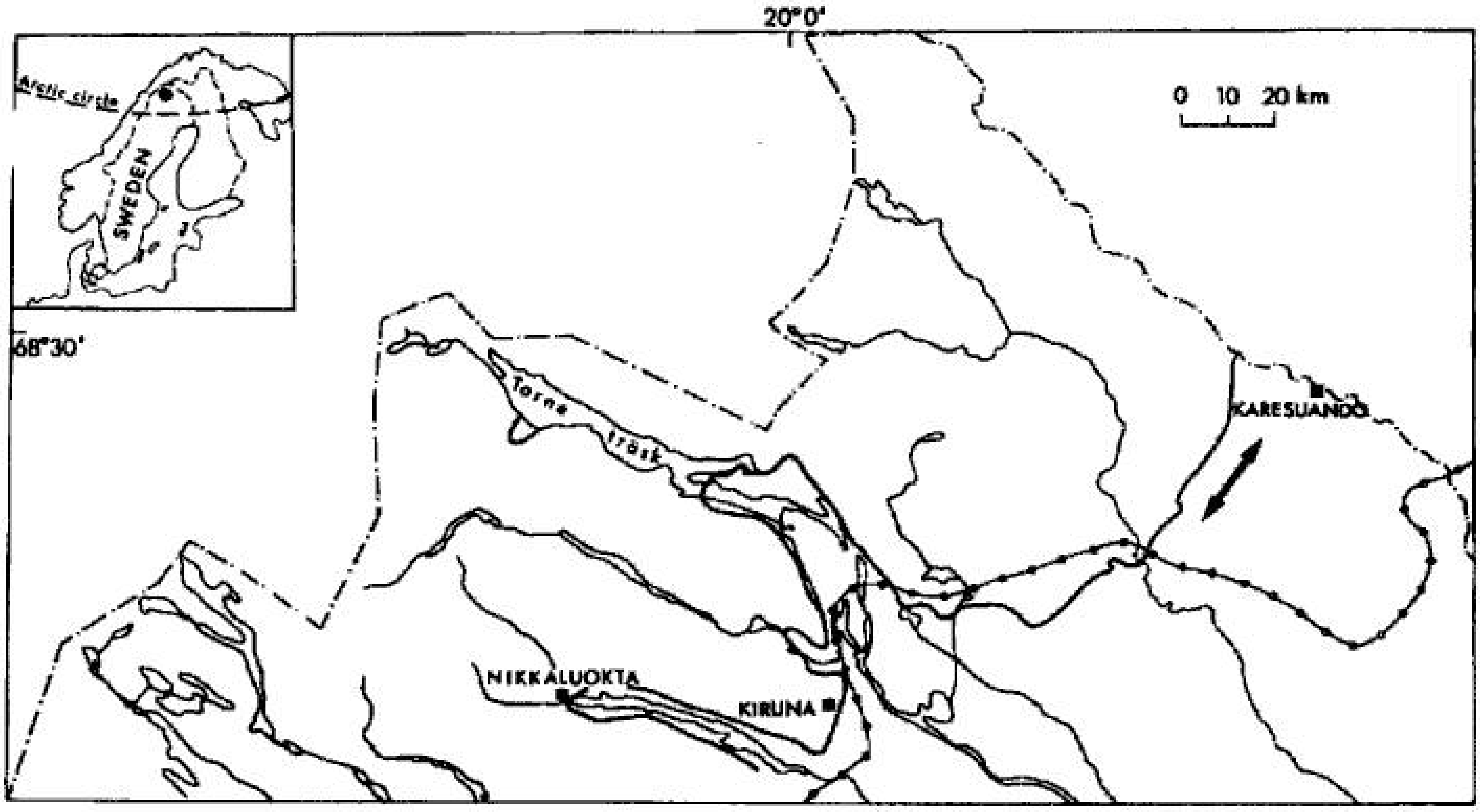

Fig. 1. Location of the study area. The transect of sample plots is indicated by the double-headed arrow.

Ehrh. spp. *tortuosa* (Ledeb.) Nyman) (Fig. 2) with scattered specimens or small groves of pine (*Pinus sylvestris* L.) (Fig. 3). Spruce (*Picea abies* (L.) Karst.) is rare in the area (Kullman and Engelmark 1991).

The basal area of pine and birch is 1 and 3 m^2 per ha, respectively. Mature pine reaches stem heights and diameters of 7-11 m and 20-70 cm, respectively. The birches are 4-6 m high.

The ground cover is a mosaic of lichen- and dwarf-shrub heath. Predominant species are *Cladonia stellaris* (Opiz) Pouz & Veda, *C. rangiferina* (L.) Wigg., *Stereocaulon paschale* (L.) Fr., *Cetraria nivalis* (L.) Ach., *Nephroma arcticum* (L.) Torss., *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum juniperinum* Hedw., *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* L., *Betula nana* L., *Arctostaphylos uva-ursi* (L.) Spreng., *Lycopodium alpinum* L., *L. complanatum* L., *Juniperus communis* L. and *Festuca ovina* L. Evidence of intensive reindeer grazing and trampling of lichen communities is ubiquitous and has rendered dwarf shrubs more prominent.

Fig. 2. Typical polycormous birch.

Fig. 3. Pine which germinated during the 1770s.

Selective cuttings, probably for fire wood, were locally noticed. Particularly at the valley bottom pine has been virtually eradicated for long stretches and birch is now dominant. At higher elevations conditions are rather pristine.

A few logs with charred stems surrounded mainly by younger trees probably reflect small spot fires. This is consistent with the conclusion by Erlandsson (1936) that forest fires played a subordinate role in these forests during recent centuries.

Methods

The pine age structure is based on a total of 70 circular plots (radius 50 m) dispersed at regular intervals along the 20 km transect. The plots cover an entire landscape segment with a representative mosaic of stand structures.

Plots with more than three remnants of felled pines or any kind of fire indication were rejected. The sample plots were placed on well-drained mineral soil.

All pines, irrespective of size, were age-determined by boring as close to the ground-level as possible or by taking stem discs at the same level for pines shorter than *c.* 2 m. This implies an error of less than five years (McCarthy *et al.* 1991). The age structure of the birch population was sampled from one representative individual within each plot. All stems (basal sprouts>1.3 m high) were age-determined similarly to pine. The tree-rings were counted in the laboratory using a stereomicroscope (x 20-40). Cross-dating was carried out visually in order to identify missing or multiple rings. The fieldwork took place during 1988-1991.

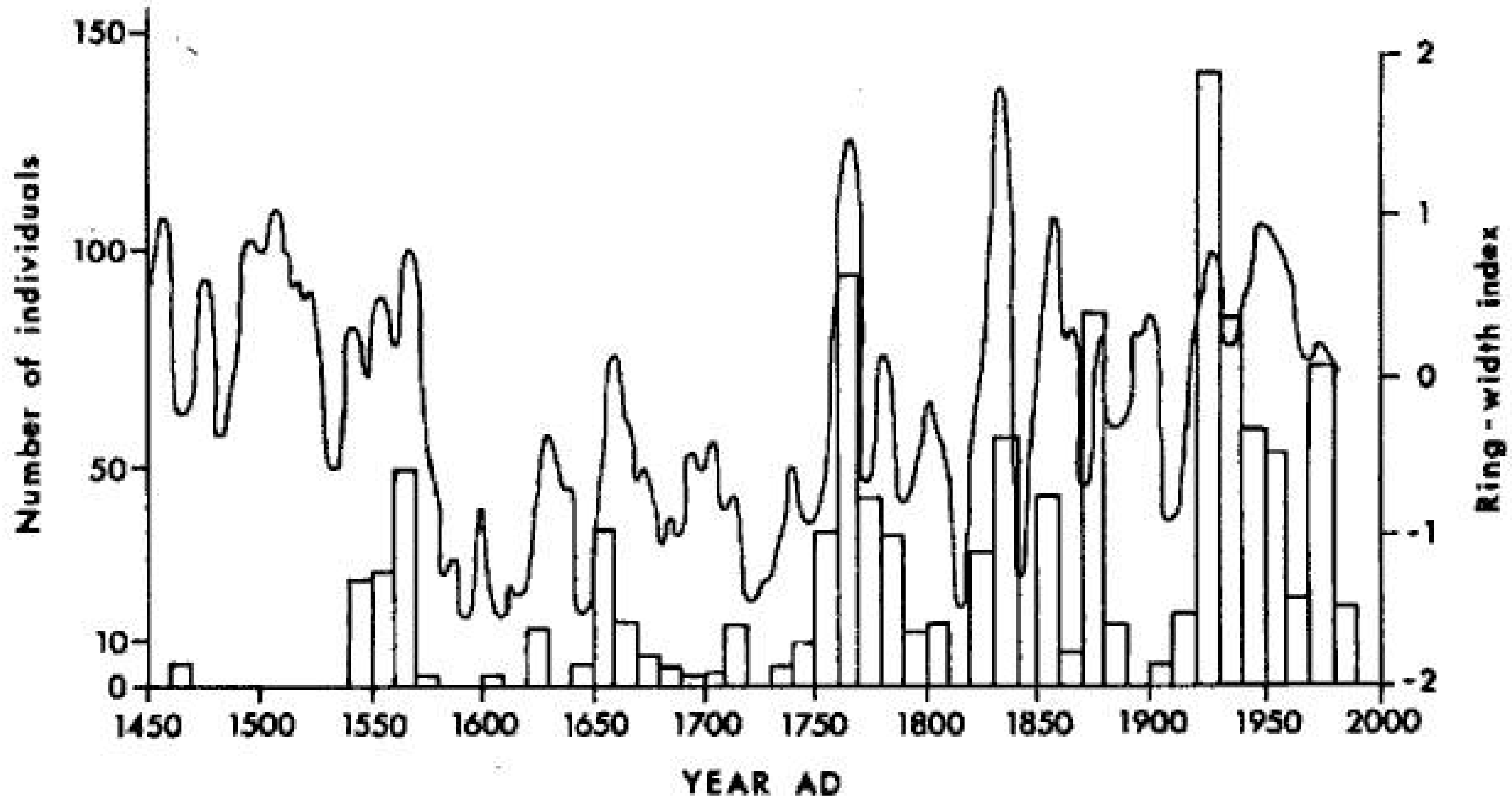

Fig. 4. Age structure of pine in ten-year age classes. The superimposed curve depicts the standardized ring- width chronology by Briffa *et al.* (in press), suggested to show the course of the April-August temperature in the region.

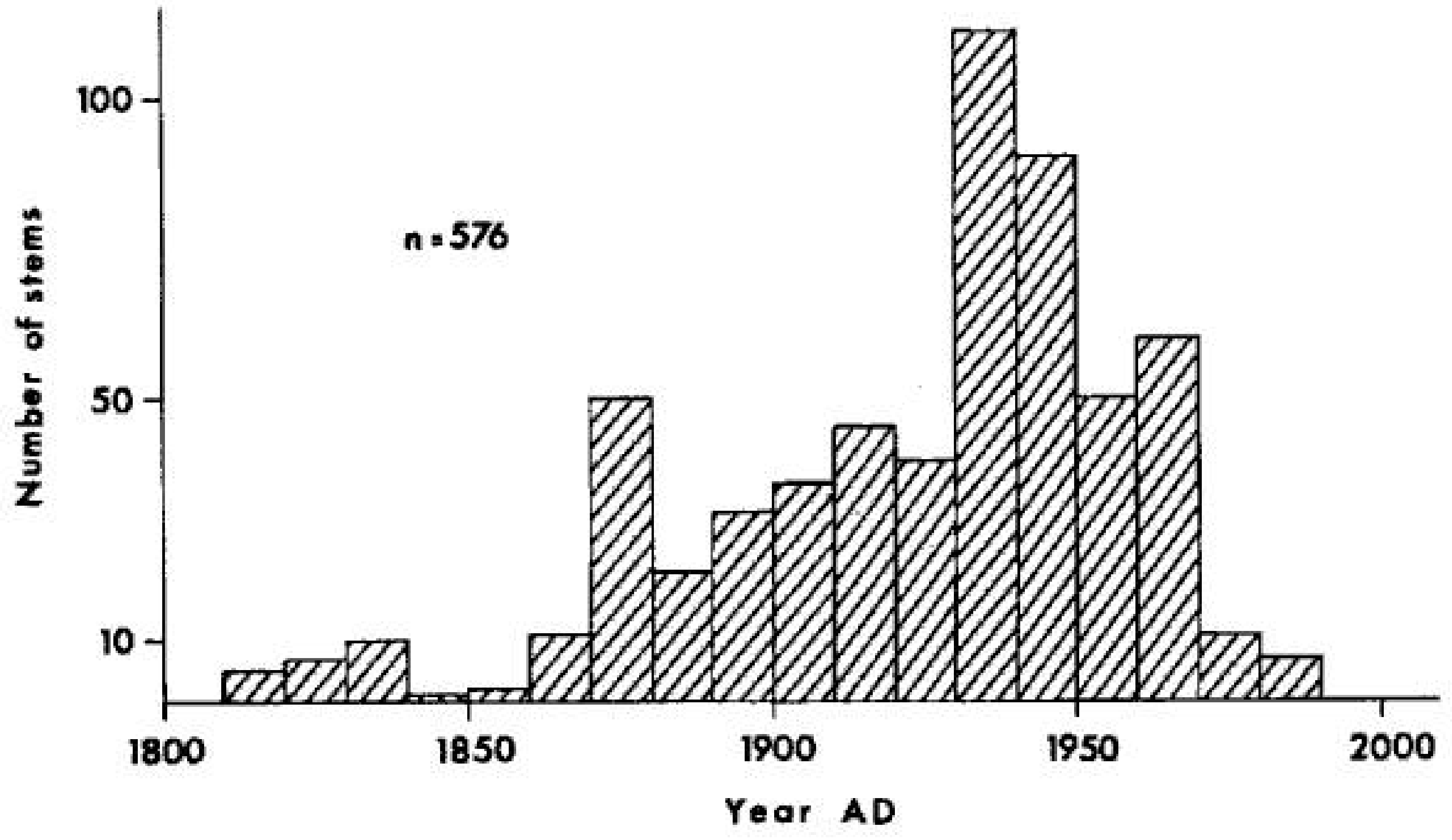

Fig. 5. Age structure of birch (stems > 1.3 m high) in ten-year age classes.

Results

The pine populations were generally sound. Dead stillstanding snags ocurred but at a low frequency and were all of great dimensions. Also decaying logs on the ground were seemingly stout. Dead medium-aged trees (50-150 years old) were rare. Wind-throws were found in more than half of the plots. Saplings shorter than 2 m were often of low vigour indicating a high mortality rate in this part of the life cycle. Spruce was not found in any of the sample plots.

A total of 1185 pines were age-determined, the oldest of which had germinated in the 1460s. The age frequency data (Fig. 4) indicates a pattern of pronounced episodic (multi-modal) regeneration. Emergent cohorts derive from 1540-1569, 1650-1659, 1750-1789, 1820-1839, 1870-1879, 1920-1959, 1970-79. Distinct regeneration gaps ocurred in 1570-1649, 1660- 1749, 1790-1819, 1840-1849, 1880-1919 and 1980-1989.

Birch displayed a more bell-shaped age structure (1810- 1980), skewed towards 1930-1949 (Fig. 5). In no case was the oldest living stem of the sampled birches younger than 80 years. Besides, decaying remnants of previously tree-sized stems were often present in the centre of the swarm of basal sprouts.

Discussion

It is fundamental that the age structure of tree populations reflects the net of recruitment and mortality (Harper 1977). Particularly in harsh climates, abundant premature dieback may occur decades to centuries after establishment (Jones 1945; Kullman and Högberg 1989, Kullman 1991b). Hence, the present-day magnitude of different age-classes does not always adequately reflect the recruitment rates, or indirectly, the contemporary ecological conditions. The meaning of the gaps, in particular, may be obscure. In the present case, however, the scarcity of dead or dying medium- aged pines suggests that this does not imply a major problem for the interpretation.

The rather high age of all sampled birch individuals suggests that the spacing of genets has remained virtually unchanged during the present century or so, although canopy closure may have increased. Similar results have been obtained from subalpine populations further south in the Scandes (Kullman 1991a). Conceivably, the bell-shaped age structure of birch results from the sampling design, leaving out low-growing basal sprouts. Sampling of all shoots of each individual would reasonably have displayed a J-shaped age frequency distribution (cf. Legere and Payette 1981), further indicating a fairly constant presence of birch over time. Possibly, the „bushy" appearance of birches bears some relation to browsing by reindeer.

Pine is much more marginal (relative to its tree-limit) than the birch and therefore the general episodic or pulsed character of its age structure is likely to indicate the decisive role of climatic variability for regeneration dynamics, quite in accord with previous deductions (Whipple and Dix 1979; Peet 1981; Morin 1986). The great importance of climate as synchronizer of regeneration close to the altitudinal distribution limit is evident also from the similarity between the present age structure and those reported from populations further south in the Scandes (Zackrisson 1985; Kullman 1987a). Most conclusive, however, is that a detailed temporal analysis reveals that the peaks of the age structure, 1540-1569, 1650-1659, 1750-1789 and 1820-1839 and 1920-59, all coincide with the highest summer temperatures according to the dendrochronological reconstruction (Briffa *et al.* in press). A large cohort emerged during the 1870s, which seems to have been a decade only slightly warmer than the long-term mean. This peak appears also in other studies (Schove 1954; Zackrisson 1985; Kullman 1987a; Steijlen and Zackrisson 1987; Ågren and Zackrisson 1990) and is also reflected in the birch age structure. A dendroclimatological study based on densitometry indicates that some summers of the 1870s were in fact relatively warm (Schweingruber *et al* 1991). This is also substantiated by meteorological records from northern Sweden (data from the Swedish Meteorological and Hydrological Institute). The regeneration peak of the 20th century was during the 1920, which was a relatively warm decade, although slightly prior to the peak of summer warmth during the 1930s, when also precipitation was relatively low (Alexandersson and Eriksson 1989). Soil drought may have hampered pine establishment during the warm 1930s. In fact, Schove (1954) concluded that radial growth of pine in northern Scandinavia responded negatively to these conditions. Alternatively, or additionally, over-crowding from the large cohorts of the 1920s reduced regeneration at later times (cf. Hett and Loucks 1976; Peet 1981). It may also be that cohorts from the 30s were selectively killed by frost drought during the 1960s which caused high sapling mortality throughout over northern Fennoscandia (Kallio, Laine and Mäkinen 1971). A similar pattern of insignificant pine regeneration during the warm 1930s is reported from the forest-limit in the southern Scandes (Kullman 1986). Grazing and trampling by reindeer may be another factor to take into account when discussing regeneration patterns in relatively modern times.

The most distinct periods of regeneration failure, namely 1570-1649, 1660-1749, 1790-1819, 1840-1849, 1880-1919 and 1980-1989 all showed relatively low reconstructed summer temperatures. For the latter two periods this is clear also from recorded temperatures (Alexandersson and Eriksson 1989).

Except for the 1650s, the whole period 1570-1750 appears to have experienced inferior conditions for pine regeneration, which broadly matches the dendrochronological results. This is in good agreement with previous delimitations of the climax of the Little Ice Age (Lamb

1982; Grove 1989). Interestingly, Tessier (1986) found that regeneration rates of *Larix decidua* in the Alps were lowered during the period 1580-1780. A broadly similar response was also recorded for *Pinus longaeva* at the tree-line in western North America (LaMarche 1973). Obviously, northern Boreal and high-elevation forests were under severe stress during these years (Nordhagen 1923; Bauer 1958; Gribbin and Lamb 1978; Eronen 1979; Lamb 1985; Payette *et al.* 1989a; Ball 1986, Kullman 1987 a, b) and maintained their positions merely be the relatively greater climatic tolerances of adults compared to juveniles and the low fire frequency in sparse populations (cf. Payette *et al.* 1989b).

It appears as if 1750 or so was a general break point, followed by increased regeneration rates at northern and altitudinal tree-limits in large parts of northern Fennoscandia (Siren 1961; Engelmark and Zackrisson 1985; Zackrisson 1985; Kullman 1986, 1987a; Boe 1991). It is less likely that this merely reflects normal ageing and dieback, since pine may attain an age of 700 years or more (Engelmark and Hofgaard 1985). In fact is has been claimed that a mostly unnoticed expansion of arboreal growth took place in northern Eurasia during the late 18th century (Bray 1971). Besides, Briffa (1992), found evidence of a common increase of forest productivity in Europe over the period 1750 to date.

The fact that *Picea abies* has not established in the study area support the view that this area is largely beyond its climatic range (cf. Kullman 1991c).

In conclusion, the present-day structure of marginal pine populations in the North and at high elevations is a consequence of accumulated population responses to past climatic variability. Competitive interactions and fire disturbance have been less influential in this environment, although not entirely absent.

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