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Rapid Natural Decline of Upper Montane Forests in the Swedish Scandes

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ABSTRACT. Unprecedented needle loss of mature forest stands occurred in natural Swedish montane forests during 1987. Pine (*Pinus sylvestris* L.) and spruce (*Picea abies* [L.] Karst.) needles turned reddish-brown during the spring and early summer. An intensive study within a severely damaged pine population indicated that damage was primarily due to a coincidence of shallow snow cover and severe cold from mid-December 1986 to mid-January 1987. This resulted in unusually cold soils and late thawing of the soils. Acute drought stress then developed in late winter during a period of sunny weather and great diurnal temperature ranges. Thus, the study supports the classical theory of winter desiccation as an important component in population ecology of cold marginal forests in this part of the world. Historical data indicate that the present kind of damage was more frequent prior to the present century. It is suggested that cold-induced dieback is an important, but often overlooked, disturbance process in northern boreal forests relevant to Holocene forest history.

Key words: forest damage, montane forests, *Pinus sylvestris* L., winter desiccation, disturbance, Holocene forest history, Sweden

RÉSUMÉ. Au course de 1987, une perte sans précédent d'aiguilles dans des bouquets de forêts adultes, s'est produite dans des forêts naturelles des montagnes suédoises. Les aiguilles du pin (*Pinus sylvestris* L.) et de l'épinette (*Picea abies* [L.] Karst.) ont pris une couleur brun rougeâtre au printemps et au début de l'été. Une étude approfondie dans une population de pins gravement touchée a indiqué que les dommages étaient dus principalement à l'existence simultanée d'une couverture de neige peu profonde et d'un froid intense de la mi-décembre 1986 à la mi-janvier 1987. Le résultat a été que les sols ont été anormalement froids et ont subi un dégel tardif. Un stress intense causé par la sécheresse s'est ensuite fait sentir à la fin de l'hiver, au cours d'une période de temps ensoleillé avec de grandes variations dans les températures diurnes. L'étude soutient donc la théorie classique du dessèchement hivernal comme étant une importante composante de l'écologie de la population des forêts marginales froides dans cette partie du monde. Des données historiques indiquent que les dommages dont il est question étaient beaucoup plus fréquents avant notre siècle. On suggère que le dépérissement dû au froid est un processus de perturbation important mais souvent ignoré, dans les forêts boréales septentrionales qui ont un rapport avec l'histoire de la forêt de l'holocène.

Mots clés: dommages à la forêt, forêts montagneuses, *Pinus sylvestris* L., dessèchement hivernal, perturbation, histoire de la forêt de l'holocène, Suède

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INTRODUCTION

The principal objective of historical plant ecology is to interpret experiments of nature and to formulate testable hypotheses (cf. Ritchie, 1984). The significance of natural disturbances, particularly stochastic events, is increasingly recognized for establishing ecological patterns (cf. White, 1979; Dury, 1980; Raup, 1981; Veblen, 1982; Foster, 1988). Climatic variability is generally experienced as the prevalent disturbance agent in temperate-boreal forests (Wein and El-Bayoumi, 1983; Delcourt and Delcourt, 1987). However, lack of good observational data on forest dynamics has induced many ecologists to postulate that forest communities below the tree-line ecotone display relatively long lags in responding to climatic fluctuations, since mature trees are supposed to resist year-to-year variations in climate (Davis and Botkin, 1985; Davis, 1986; Brubaker, 1986). However, most experiments and observations emerge from a climatically anomalous period — that is, the present century — which until recently has been exceptionally warm and climatically stable (Bryson, 1974; Jones *et al.*, 1986; Wallén, 1986). The current ecological theory of forest dynamics may be biased, since palaeoecological studies also have mainly addressed range extensions resulting from climatic amelioration.

The present paper reports a case study of the regional decline of upper montane coniferous forests in Sweden, which accelerated during 1987. Here we document an older natural population of pine (*Pinus sylvestris* L.), which developed almost total foliage discolouration during 1987.

Recent forest decline has been observed along the entire range of the Swedish Scandes (c. 900 km) and also in northern Finland. Cursory survey journeys and communication with foresters and other observant persons indicate that within the uppermost 100 m of the montane forest belt conifers lost approximately 30-50% (locally even more) of their needles in 1987 (Kullman, in press). In certain places, stands 200-250 m below the coniferous tree limit were damaged. In general, spruce (*Picea abies* [L.] Karst.) has suffered more extensively than the pine, which exhibits more severe damage within local areas. Except for results of insect outbreaks, dieback of the present dimension and rapidity of mature primaeval forests has not previously been studied directly in northern Scandinavia or reported elsewhere in boreal forests. Less severe damage, involving mostly the youngest needles of saplings or young trees, has been observed in Scandinavia now and then during the 20th century (Andersson, 1905; Langlet, 1929; Venn, 1970; Kallio *et al.*, 1971). Close to the tree limit, however, needle kill of exposed solitary individuals during winter and spring is a recurrent feature of the entire northern hemisphere. The relative importance of winter desiccation versus direct frost in this connection is still controversial (Sakai, 1970; Marchand and Chabot, 1978; Tranquillini, 1979, 1982; Wardle, 1981; DeLucia and Berlyn, 1984).

STUDY AREA

General Overview

The study was carried out in the southern Scandes, Sweden (Fig. 1), at the mouth of the Handölan Valley (63°16′N, 12°25′E). Phytogeographically it falls within the Northern

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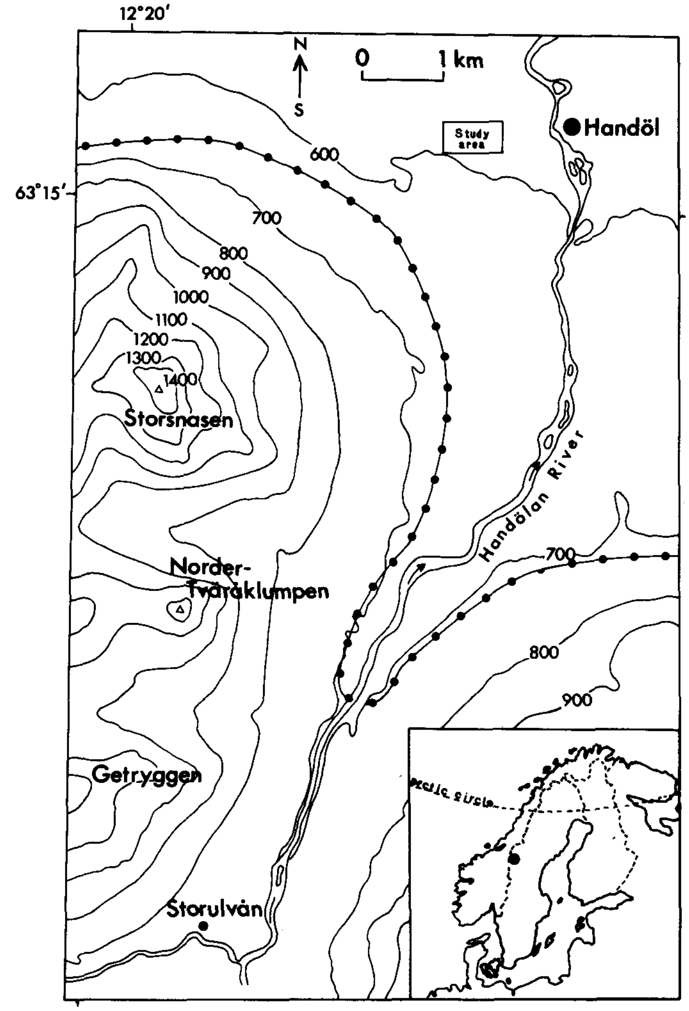

FIG. 1. Location of the study area. The tree limit of *Pinus sylvestris* is indicated by the dotted line.

Boreal zone (Ahti *et al.*, 1968). The sampling site was on the NE-facing flank of Mt. Storsnasen, which rises to 1463 m a.s.l. Below the slope a wide basin with a great lake (Ånnsjön) extends to the north, west and east, at an altitude of 530-600 m a.s.l. The bedrock consists of amphibolite. Quaternary deposits are peat and ice-dammed lake sediments (mostly fine sand), with traces of glacifluvial erosion (Lundqvist, 1969). Data from the nearest meteorological station (Storlien/Visjövalen, 642 m a.s.l., 12 km northwest of the study site) indicate that the climate of the region has a local maritime character. Mean annual temperature is +1.1°C, with a mean monthly temperature of −7.8°C in January and +15.5°C in July. Mean annual precipitation is 1012 mm. All data refer to the period 1931-60. This station is approximately at the same altitude as the sample plot, the climate of which is slightly less maritime in character due to a steep west-east gradient in maritime-continental nature (Kullman, 1979). Hence, daily minimum and maximum temperatures at the sample site are lower and higher respectively, and the snow cover is more sparse and less lasting. Observations during 1988 showed that the snow depth at the sample site was c. 25% lower than at Storlien/Visjövalen.

Below the alpine zone subalpine woodland with *Betula pubescens* Ehrh. subsp. *tortuosa* (Ledeb.) Nyman is succeeded downslope by montane stands of mainly *Picea abies* and *Pinus sylvestris*, mixed with mires. The local tree limits (i.e., trees >2 m high) for birch, spruce and pine are 865, 800 and 670 m a.s.l. respectively. No traces of forest fires or tree cutting have been found in or close to the study site. Additional data on the study area and its setting are provided by Kullman (1979, 1983a).

Weather Anomalies 1985/86 and 1986/87

Weather conditions predating the occurrence of damage are described as a basis for evaluating the causes of the dieback pattern. From Figure 2A it is clear that the late autumn of 1985 and early winter of 1986 were much colder than the mean for the so-called normal period 1931-60. May and June 1986 were c. 2°C warmer than the standard of the above period, while July-August experienced a temperature deficit of the same magnitude. November was relatively warm. December (1986) and January (1987) showed the same pattern of subnormal temperatures as one year previously. This period around the turn of the years 1985/86 and 1986/87 was in fact among the coldest during this century in great parts of Sweden (Eriksson, 1987; Larsson-McCann, 1987). February was normal, while March was relatively cold. From May to September all months were colder than the mean for the period 1931-60.

Figure 2B presents snow depth measurements at Storlien/Visjövalen on the 15th and last day of each month for the same period as the temperature data. In 1985/86 snow was consistently deeper than normal, except at the very end. A particularly striking feature of 1986/87 was the subnormal snow depth from October until mid-January. However, later during that winter the snow was much deeper than usual. The last melting phase in the spring was delayed. Observations very close to the study site in early January 1987 showed that exposed areas were practically free of snow. The average snow depth was estimated at less than 10 cm.

The long-term data of snow depth and temperature (1963/64-1986/87, which is the full extent of recordings) indicate a unique coincidence of abnormal cold and shallow snow cover in December 1986 and early January 1987 (Table 1). The weather conditions during the winter/spring 1986/87 are depicted in finer detail in Figure 3. Daily measurements of snow depth are presented in 3A, while 3B gives the daily maximum and minimum temperatures. The duration of the extreme weather period was mid-December to mid-January. The lowest temperature, −33.2°C, was reached on 11 January, when the snow cover was 39 cm at Storlien/Visjövalen. The extreme cold terminated gradually in late January and early February. Additionally, Figure 3B shows the general character of the weather each day, namely, predominantly clear skies or cloudy. It is evident that the first five months of 1987 were on the whole exceptionally cloudy. The longest continuous periods of sunny weather occurred in January and March.

METHODS

Sample Plot

A 0.5 ha sample plot was established at an altitude of 570-580 m a.s.l. It was selected to cover a representative forest stand of predominantly *Pinus sylvestris* that experienced rapid dieback in 1987. The height of the overstory was 7-9

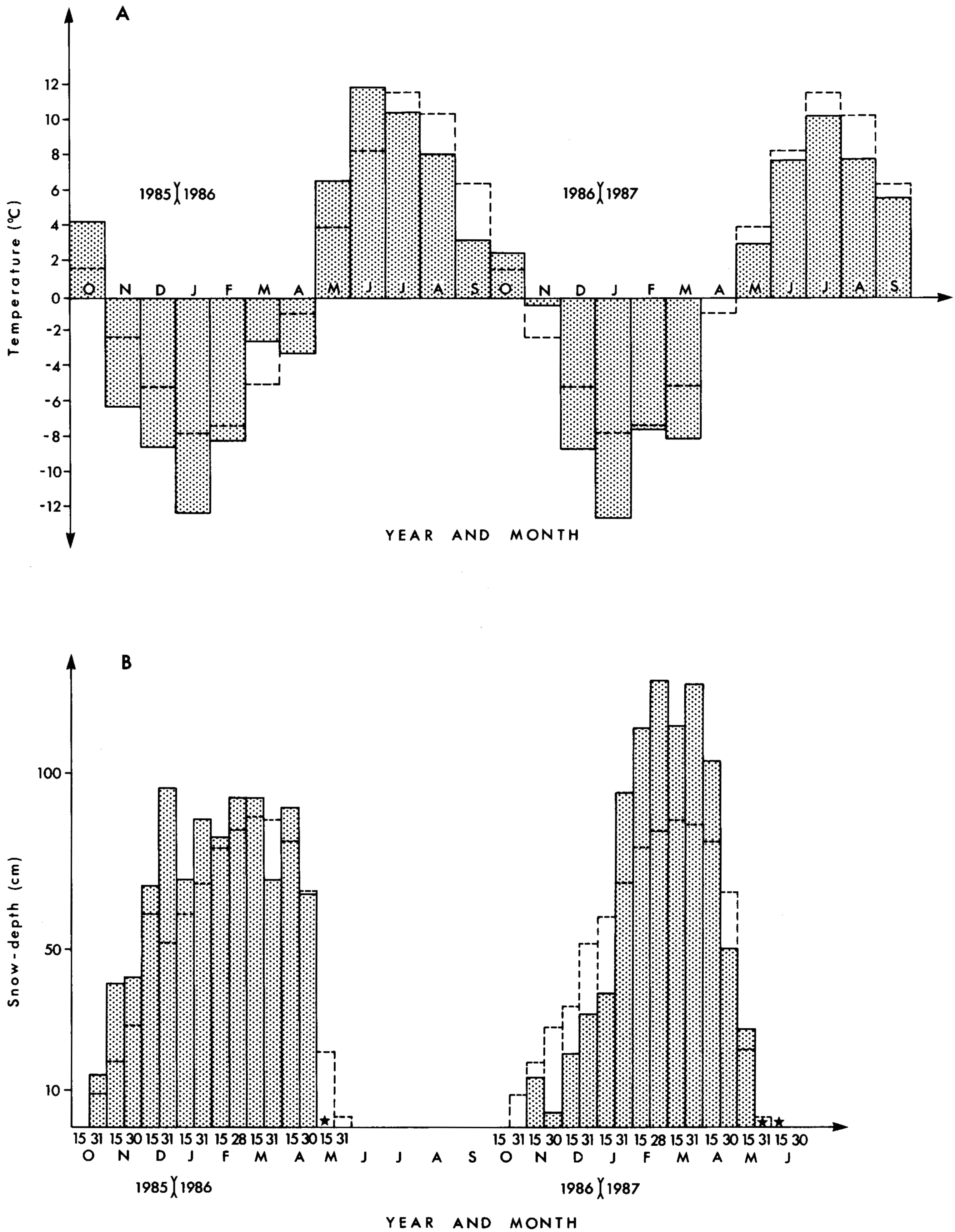

FIG. 2. Meteorological data from the Storlien/Visjövalen meteorological station. A) Mean monthly temperatures. The respective means for the 1931-60 period are given by a dashed line. B) Snow depth on the 15th and last day of each month. The respective means for the period 1961/62-1986/87 (maximum extent of observations) are given by a dashed line. Discontinuous snow cover is indicated by ★.

TABLE 1. Annual data of mean snow depth (15 and 31 December and 15 January) and mean temperature (December-January) for the Storlien/Visjövalen meteorological station

Year	Snow depth (cm)	Temperature (°C)
1963/64	46	−3.3
64/65	52	−6.4
65/66	52	−12.0
66/67	31	−7.8
67/68	14	−8.4
68/69	24	−5.6
69/70	57	−8.8
70/71	23	−3.6
71/72	45	−5.7
72/73	15	−1.0
73/74	68	−4.2
74/75	48	−4.0
75/76	124	−5.8
76/77	44	−6.5
77/78	33	−4.9
78/79	57	−13.5
79/80	35	−8.5
80/81	96	−7.4
81/82	40	−11.4
82/83	30	−4.0
83/84	93	−7.6
84/85	39	−7.5
85/86	78	−10.5
86/87	30	−11.7
Mean	49	−7.1

m, with a few specimens reaching 11 m. Dead standing snags or trunks on the ground did not exist in the study plot. The pines were aggregated to certain sections, which probably reflects different hydrological conditions and/or snow depths. A striking feature was that saplings (pines <2 m high) practically never appeared beneath the crown projections of tree-sized pines. Scattered spruces, most of which were less than 2 m high, and tree birches grew in the sample plot.

The plot extended from a mixed mire to its transition to ordinary well-drained podzolic soil. Distinct "islands" with the latter soil type occurred in the mire matrix. The maximum peat depth was c. 1 m, but more than 90% of the pines grew on shallower peat. Practically all the tree-sized specimens occurred on ground with less than 0.3 m peat.

The ground was mainly sloping northward and densely strewn with low peat hummocks (relative amplitude 0.3-0.5 m). Characteristic species were *Calluna vulgaris* (L.) Hull., *Rubus chamaemorus* L., *Equisetum sylvaticum* L., Vaccinium *uliginosum* L., V. *myrtillus* L., *Oxycoccus microcarpus* Turcz., *Carex pauciflora* Lightf., *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum affine* Func., *Dicranum bergeri* Bland., *D. elongatum Schwaegr.,* and *Sphagnum fuscum* Schimp. Klinggr. In depressions *Eriophorum vaginatum* L. and *Scirpus caespitosus* L. were prevalent. On well-drained sites, particularly beneath the crowns of the older pine trees, the ground cover included *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* L. and *V. myrtillus*.

Observations in January and February 1988 (above normal snow depth) showed that the snow cover had a wide spatial variation in thickness, ranging between 0.1 and 1 m. Pine saplings never occurred where the snow cover was thinner than 0.2 m. Studies during earlier years (1972-83) in the same area and within the sample plot in January-March 1988 revealed freezing in the winter to be confined to the uppermost decimeter of the soil, or even lacking at certain spots. In general soil frost has disappeared during April in the interspaces between the trees and in June beneath the crowns of old pine trees. In no case, except in 1987, has the root zone been frozen later than mid-May.

Population Structure and Tree Vigour

The location of each pine was mapped and the ages of all individuals higher than 2 m were estimated by counting the annual rings at the root-trunk junction. Sampling was carried out with an increment borer, a method considered to give the best indication of the true age of trees (Tucker, 1983). Pines shorter than 2 m were dug or pulled up from the soil, and ring counts were made on transverse sections at the root collar. Height of the larger pines was estimated with a measuring rod or a SUUNTO tree-height meter.

For each of the pines within the study plot the degree of injury in 1987 was assessed as the percentage of needle browning. Classification to the nearest 5% was carried out in September 1987, when dead needles were still not shed. The uncertainty of this kind of estimate for tall trees is thought to be in the order of 10% (Westman and Lesiński, 1986). In the present case, however, most individuals were relatively small, and hence the uncertainty was probably less. Needle discolouration estimates were checked against estimates that had been accurately determined from photographs.

Statements concerning significant differences are based on the t-test, the level of significance being 0.1%.

RESULTS

General Observations

The damaged pine forest, with its entirely reddish-brown crowns, made a spectacular impression (Fig. 4). Spruce trees in the plot were also severely damaged (Fig. 5), and their needles were shed in the early summer in 1987. Some birches and aspens (*Populus tremula* L.) failed to develop leaves during the entire summer. Buds dried before the new leaves started to emerge. *Juniperus communis* L., *Empetrum hermaphroditum* and *Calluna vulgaris* showed extensive browning within the study plot.

Crown damage occurred principally between 565 and 580 m a.s.l. Also pines at altitudes higher than the plot were discoloured, although not as intensely as within the study plot. During ongoing monitoring at the tree limit (c. 100 m above the study plot) in this valley (cf. Kullman, 1983b), few signs of new damage were recorded in 1987. The first indications of extensive damage in the study area were noted in May 1987. Discolouration of all year-classes of needles then developed from yellowish to reddish-brown. Most needles were not shed by September 1988, although they had turned more brownish. No signs of fungal infection were discovered until 1988, when already dead needles were affected by *Phacidium infestans* Karst.

A particularly notable feature on the pines, where almost 100% of the foliage had died, was that the current year's buds and shoots were not visibly damaged (Fig. 6). Certain phases of the phenological development were delayed compared with undamaged nearby populations at the same

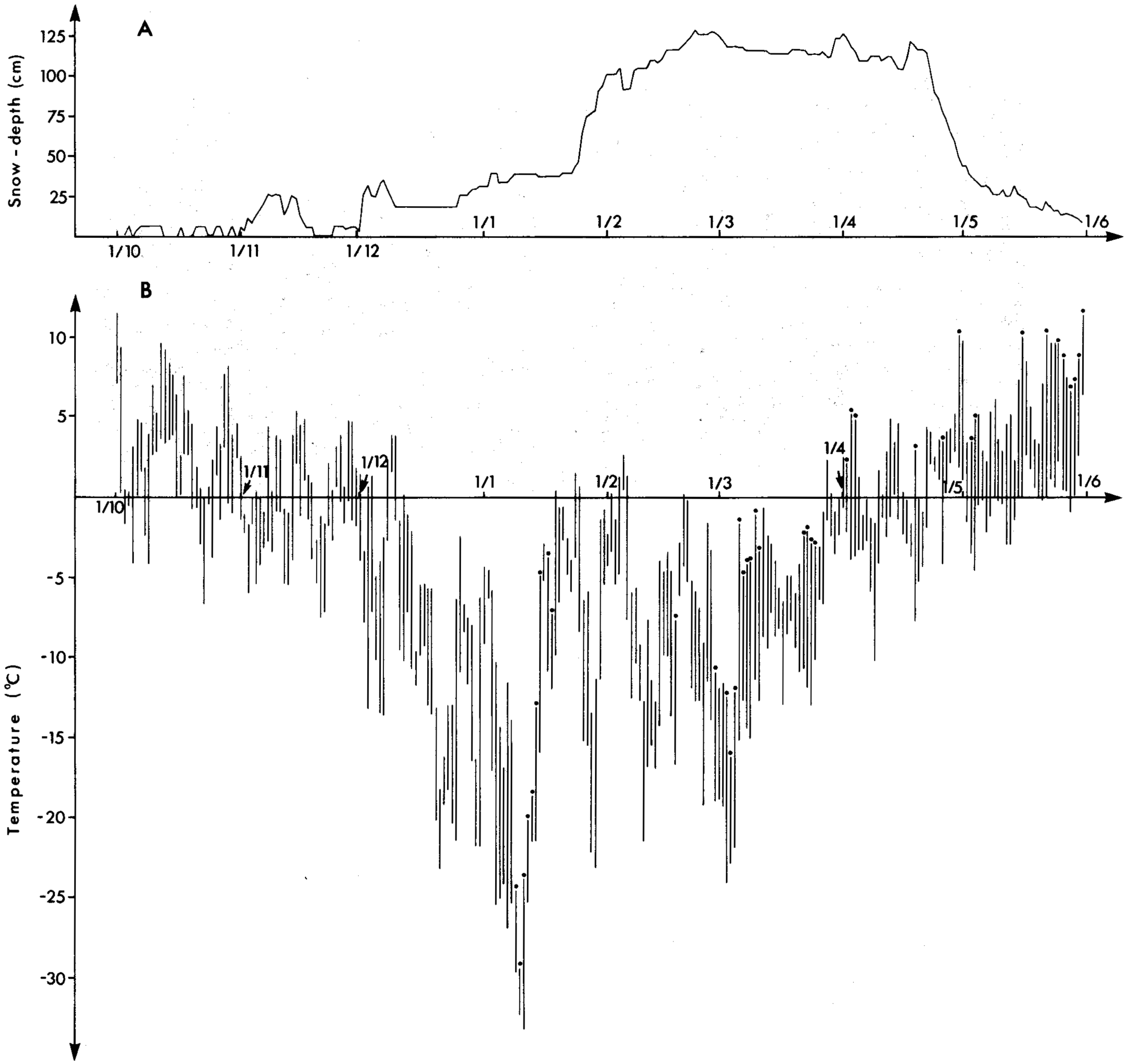

FIG. 3. Meteorological data from the Storlien/Visjövalen meteorological station. A) Daily snow depth values. B) Daily maximum and minimum temperatures. Days with prevailing clear skies are denoted by •, absence of which indicates that the day was mainly cloudy (1/12-31/5).

and even higher altitudes. Bud break occurred in mid-July, and still in early August the annual shoots of laterals were not longer than c. 1 cm, while undamaged trees had new shoots within a range of 3-5 cm.

Excavations of different sized pines showed that they had very shallow and mainly lateral root systems. Practically no roots were located below 0.3-0.5 m. Seedlings and saplings had more surficial roots than trees.

In early July 1987 the soil of the whole sample plot was frozen beneath an active layer of 2-3 dm. The thickness of the frozen soil layer, which included thin lenses of pure ice, was 1-3 dm. In early August the ground was completely thawed except in peat hummocks, which thawed by early October.

Pine dieback had not progressed perceivably in 1988, which was a relatively warm year (winter, spring, summer), and thawing of the root-zone was completed in April-May. The needles on surviving shoots were 2-3 times longer in 1988 than in 1987.

Age Structure of the Population

The age structure of the population is shown in Figure 7. The oldest tree, which dates back to the 1760s, was only lightly damaged. Since the early 19th century a small number

FIG. 4. A section of the severely damaged pine forest within the study plot. The reddish-brown colour developed in late spring and early summer. Large trees had significantly higher percentage of dead needles than small individuals.

FIG. 5. A spruce stand that suffered more than 90% needle loss in 1987.

FIG. 6. Many pines lost all needles during 1987. The photo shows current year's shoots, which were dwarfed and phenotypically delayed. Photo: 1988-01-08.

of pines have reached maturity. More than 80% of the present population, however, originates from the post-1950 period. The numbers of the latest age-class are not comparable with the earlier ones, since it only represents 7 years. On a broad scale the age distribution conforms to the reverse J-shaped depletion model (Harper, 1977). Thus, during at least the past 100 years recruits appear to have steadily balanced deaths. Some decades during the mid-19th century are likely to have experienced quite abundant regeneration, although the survival has been low.

Assessment of Damage

Table 2 shows the percentage needle loss for four ranges of plant heights. Needle loss increased significantly with increasing height of the pines. Not a single pine higher than 0.5 m escaped damage. On the other hand, a large proportion of the individuals in the class <0.2 m were undamaged and quite healthy. More than 80% of the pines in the class 0.21-0.50 m had their injuries distinctly confined to the upper part of the crowns. Table 3 presents the aspect of the undamaged part of the crown for pines >2 m high. Shoots and needles facing the northerly sectors more frequently survived injury to the population (Fig. 8). The same general

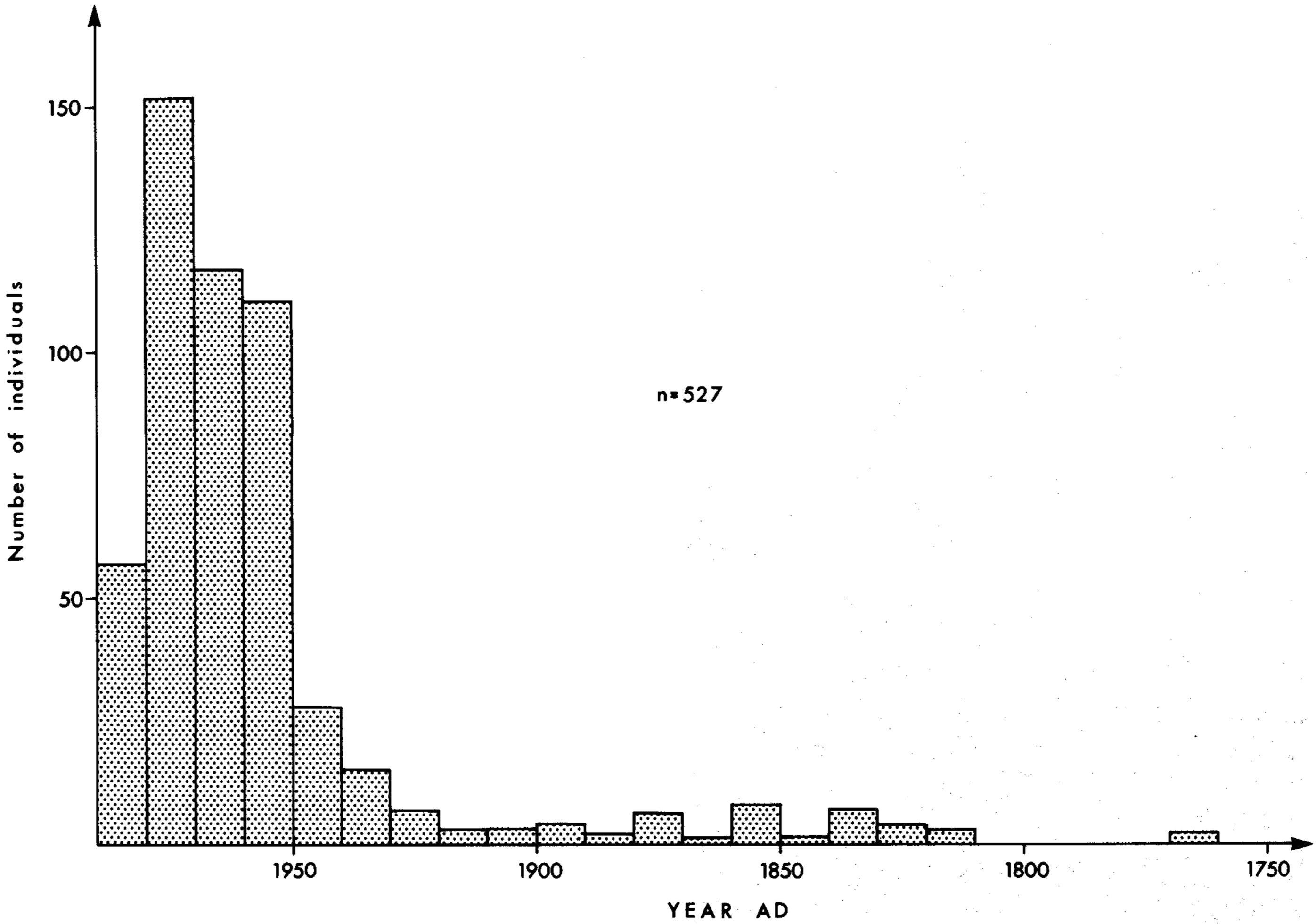

FIG. 7. Age of the pine population in ten-year frequency classes.

TABLE 2. Percentage needle loss for four height classes of pine

Height range (m)	Needle loss ($\bar{X}$ ± S.D., %)	n
≤0.20	6 ± 16	70
0.21-0.50	29 ± 27	96
0.51-2.00	49 ± 27	287
>2.00	80 ± 22	74

TABLE 3. Aspect of the undamaged part of the crown for all living pines >2 m high

Aspect	Number of pines
N	49
NW	3
W	1
SW	—
S	—
SE	1
E	7
NE	8

pattern of height-injury relationship was observed among the spruce trees growing in the plot.

DISCUSSION

The observations indicate that climatic factors were primarily responsible for the dieback process. If, for example, atmospheric pollution had been a predisposing factor by affecting the winter hardiness (cf. Hinrichsen, 1986), it would be hard to explain why damage to pine was restricted to peat soils with late thawing and why epiphytic lichens are still growing vigorously on dead twigs.

Contrary to the present results, earlier studies have demonstrated that seedlings and saplings are generally more easily damaged by climatic stress such as surface frost (e.g., Eiche, 1966; Tranquillini, 1979; Kullman, 1981; Hadley and Smith, 1983; Havas, 1985). This anomaly suggests that some infrequent environmental factor or combination of factors has been operative. The exceptionally late thawing of seasonal ground frost in 1987 was such an unusual event with potential impact on tree vigour. In 1987 new discontinuous permafrost developed in peat at altitudes just a few tens of meters above the sample plot (Kullman, 1988b). This permafrost was short-lived, however, and had disappeared in July 1988. The lack of new damage in 1988 and vigorous needle growth that year support the idea of a single causal event in 1987.

FIG. 8. Northerly sectors of the crowns of certain pines were only slightly damaged.

From a 20th-century perspective, permafrost and the extension of seasonal ground frost until late August is quite an unusual event in this part of the Scandes (cf. Lundqvist, 1969). Old documentary accounts, however, indicate that late thawing previously prevented pine establishment and episodically exterminated pine growth in this particular region. In 1889 an agro-botanist, Ernst Henning, surveyed these parts of the Scandes. Henning (1895) noticed that most older pines were dying, particularly on mires slightly below the forest limit. He also visited the study area (±1 km from the sample plot) and observed pine saplings, but stated that they seemed to have small chances of survival. The reason was obvious to him, namely, the presence of frozen soil at a depth of 0.3-0.4 m in mid-August. These observations are consistent with some features of the present age structure (Fig. 7).

The pronounced episodic nature of regeneration during the 19th century suggests that the study site was more marginal at that time than during the 20th century. Some regeneration peaks around the mid-19th century were possibly responses to short periods of warm summers, such as in the 1850s, when winters were still much below 20th-century levels (Liljequist, 1970). Thus, late seasonal thawing may have checked the saplings when they reached a certain height, exactly as happened in 1987, possibly explaining why so few have survived until recently. It is worth noticing that during some previous years of extensive pine damage in northern Sweden, such as in 1903 and 1928, seasonal frost was exceptionally deep (Andersson, 1905; Langlet, 1929).

The character of the habitat of the study area, i.e., a NE-facing slope with hummocky peat, is exactly the kind of ecological setting most likely to thaw late and to favour formation of new permafrost (Viereck, 1973; Tyrtikov, 1978). Since areas with damaged spruce and birch have a spatial continuity with the pine population of the study area and damage developed simultaneously, it is reasonable to suggest that the basic mechanism was similar. In this type of environment pine has relatively surficial roots, enhancing sensitivity to soil frost. At the altitudinal tree-limit, pines are mostly growing on dry mineral soils and are more deeply rooted. This circumstance may explain why they were relatively little affected by the 1987 event.

The abnormal (20th-century perspective) cold and shallow snow cover from mid-December until mid-January induced soil frost of exceptional degree, depth and duration. As snow depth of the study site was less than one decimeter, it is not likely that the temperature of the surficial soil layer deviated much from the air temperature (cf. Ylimäki, 1962; Brown and Péwé, 1973). When the soil temperature is below 0°C, a decreasing fraction of the soil moisture is available to the roots (Rydén, 1986). It is likely that this fraction was uniquely small in 1987, which may have contributed to the severe damage. The relatively rapid build-up of a deep snow cover after mid-January could have extended the extremely low soil temperatures for the entire winter (cf. King, 1986).

Since all year-classes of needles were equally damaged, it is a reasonable assumption that the mechanism of damage involved a complete drought stress (cf. Holzer, 1959).

Observations in 1988 indicated that snow interception within the study site is a function of individual stature (Fig. 9), which in part explains why large pines were more severely damaged than smaller individuals. Even for most solitary tree-sized pines, the maximum snow depth beneath the crown projection is less than half the value in the open. Scott *et al.* (1987) similarly concluded that root zone temperatures of trees close to the arctic tree line are influenced by tree age (stature), since snow interception, shade during the summer and thickness of organic soil layer are all positively correlated with tree age (cf. Viereck, 1965; Zoltai and Tarnocai, 1971). Possibly smaller individuals with a large proportion of their foliage buried in the snow could replenish their water losses through foliar absorption of water vapour beneath the snow. Thus, contrary to the normal situation, the large trees, with their foliage high above the snow surface, may have exhausted their stored water reserves during the extreme winter of 1987 (cf. Marchand, 1987).

The first sign of needle damage appeared in early May, and the buds were undamaged but phenologically delayed. These circumstances suggest that drought stress was acute well before the normal time of bud flushing in early June. Delayed bud flushing seems to be a general response to poor snow cover and cold soil (Frey, 1983). Plant tissues with relatively low water content, e.g., buds, did not suffer, pointing to the importance of drought stress rather than, for example, frost damage. Water may have become unavailable even to roots penetrating beneath the frozen soil layer, because

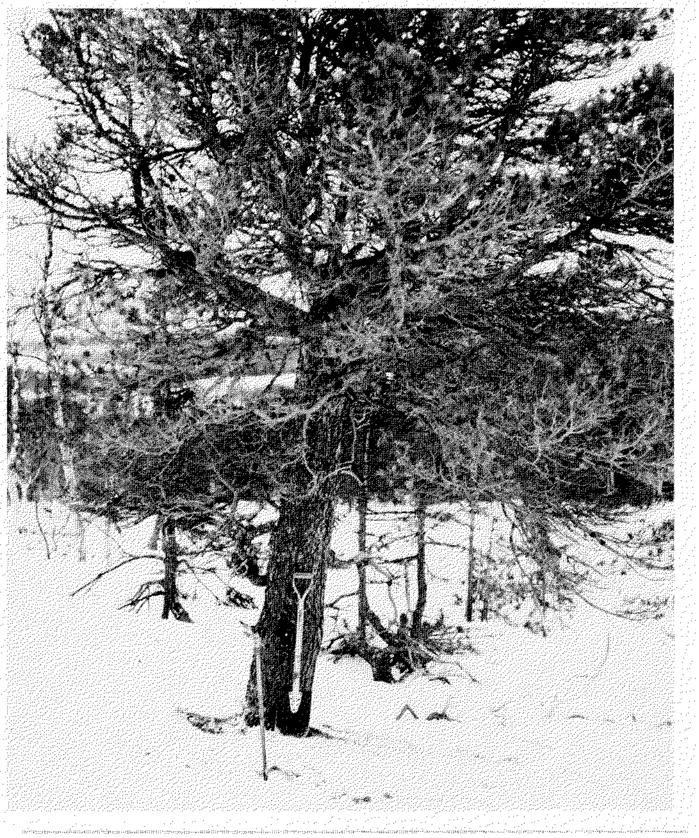

FIG. 9. The snow depth is significantly reduced beneath the crowns of the pines. During mid-February 1988 the snow depth was 15 cm or less and the ground was frozen to a depth of 20 cm. The early winter of 1988 was mild and the snow cover deeper than normal. In 1986/87 the frost penetrated at least 0.5 m beneath the ground surface.

moisture in both peat and mineral soil is transported upward and stored in the frozen layer (Juusela, 1967).

Since foliage facing NE exhibited less damage than foliage in other aspects, it seems that dehydration and/or excessive build-up of heat, due to sunshine, was one part of the mechanism of damage. Since pines 0.21-0.5 m high were frequently damaged only in their tops, one may conclude that damage was initiated before the snow had started to shrink appreciably. Strong solar radiation occurred during the first half of March, when weather became clear, with large diurnal temperature variations (Fig. 3B). Particularly between 6 and 11 March the daily maximum temperatures could have exceeded 0°C in exposed plant tissues, although the temperature at the standard meteorological level was a few degrees below zero (Christersson and Sandstedt, 1978). Similar periods with clear days occurred again toward the end of March and during the first days of April. The meteorological records at Storlien/Visjövalen give no indication of sudden warm air incursions ("foehn-effects") during the winter, which could have induced needle kill (MacHattie, 1963; Aulitzky and Turner, 1982).

The severity of damage in 1987 may have been enhanced due to the accumulated effects of climatic stress during recent decades (cf. Friedland *et al.*, 1984), which in fact have induced retrogression of tree populations (birch and spruce) within the tree-limit ecotone of the study area (Kullman, 1988a, 1989). In this region mean temperature for 1978-87 of July-August was 0.8°C lower and of December-January 3-4°C lower, compared with 1931-40 (Eriksson, 1988).

Although limited to a single field study, the results support the classical theory of winter desiccation (Kihlman, 1890; Michaelis, 1934) as an important mechanism in cold marginal tree population dynamics (cf. Sakai, 1970; Tranquillini, 1979, 1982). This study of unprecedented forest dieback shows that mechanisms of rapid natural forest retrogression exist below the tree-line ecotone. Earlier postulates of climatically induced forest dynamics in continuous forest zones as smooth processes, relatively insensitive to year-to-year changes of climate parameters (e.g., Davis and Botkin, 1985) are not of general validity (cf. Gajewski, 1987). The severe destabilization of an entire ecosystem was, in fact, triggered by abnormal weather during a very short period of time. Except for "wave-regenerated" forests (Sprugel, 1976), cold-induced mortality of mature stands may be a much overlooked process in northern and montane environments, possibly causing intermittent breaks in the ecological successions (cf. Kullman, 1987a,b). The climatic favourability and stability of this century up to now may explain why this is not well documented. This indeed provides a new perspective to inferences from paleoecological data within historical plant ecology.

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