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Damage to *Pinus contorta* in northern Sweden with special emphasis on pathogens

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Abstract

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During a nine-year-period ca. 100 provenances of *Pinus contorta* were investigated annually with respect to different kinds of damage, primarily by parasitic fungi. Damage to *Pinus contorta* occurred mainly during the first ten years after planting. northern provenances of *Pinus contorta* were generally more resistant to pathogens than southern provenances. Weather damage occurred almost every year among trees of southern and coastal provenance. Trees of northern provenance also suffered from weather damage due to temperature oscillations during shoot elongation.

Severe weather damage predisposed to infection by secondary pathogens, primarily *Gremmeniella abietina.* Even northern provenances of *Pinus contorta* were infected by *Phacidium infestans* in high-altitude stands in northern Sweden. Snow blight infection was, however, of less importance to lodgepole pine than to Scots pine, owing to the rapid early growth of the former. The most productive plants of both *Pinus contorta* and *Pinus sylvestris* were attacked by *Phacidium infestans.*

So far vole damage has been the most severe threat to *Pinus contorta* in northern Sweden. Severe infection by *Gremmeniella abietina* was recorded after vole attack, even among northern provenances of lodgepole pine. Hitherto *Pinus contorta* has mainly been infected by the same fungi as *Pinus sylvestris,* with the exception of *Melampsora pinitorqua* and *Lophodermella sulcigena.*

Key words: Pinus contorta, Pinus sylvestris, provenance, weather damage, vole damage, parasitic fungi, *Gremmeniella abietina, Phacidium infestans,* Sweden.

ODC 443:174.7 *Pinus contorta.*

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Introduction

In the past decade the lodgepole pine, *Pinus contorta* Dougl. ex Loudon, has become increasingly important for Swedish forestry. Eighty million lodgepole pine seedlings are planted every year in northern Sweden, compared to 2 million in Norway and 1.5 million in Finland. The reason for this wave of enthusiasm for *Pinus contorta* is that Swedish forest industry has been looking for a tree species, which grows more rapidly than the native Scots pine (*Pinus sylvestris* L.), so that the shortage of raw material for the pulp industry, which is expected to occur at the turn of the century, can be compensated for. The optimum rotation of lodgepole pine is considered to be 15–20 years shorter than that of Scots pine (Remröd, 1977).

The problems related to the introduction of foreign tree species have already been briefly reviewed by the author (Karlman, 1981) and have, for decades now, been discussed by pathologists and geneticists (Boyce, 1954; Peace, 1962; Pawsey, 1974; Kiellander, 1976; Karlman, 1976, 1978; Burdekin & Phillips, 1977; Phillips, 1979; Hayes, 1980; Stephan, 1980; Martinsson, 1980; von Weissenberg, 1982).

It is hard to judge how great the risks of epidemic outbreaks are in the case of the lodgepole pine. According to ecological theories, a recession will occur sooner or later (Harper, 1977). It is, however, clear that the period during which *Pinus contorta* has been tried out in Scandinavia is too short for it to be possible to foresee future developments with any certainty. In the case of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) in central Europe, fungal epidemics first occurred about 90 years after it was first planted and 40 years after its more extensive cultivation. Similar results were reported for *Pinus strobus* L. Considering that the occurrence of single extreme anomalies, within the natural climatic range, may be of decisive importance for the survival of an introduced tree species, it must be pointed out, that *Pinus contorta* has not yet been exposed to all the extreme weather conditions that can occur in northern Scandinavia within the rotation period of a conifer. The first plantations of lodgepole pine in Sweden were in fact established during a period (1930–60) when the most favourable climate recorded during the past 1 000 years prevailed (Gribbin & Lamb, 1978).

From the results of many years of provenance research we know that the correct choice of provenance is of utmost importance for the success of any exotic tree species (cf. Karlman, 1981). Despite the occurrence of the severe fungal epidemics in Central Europe during the 1920's, the Douglas fir has nevertheless become the most important exotic tree species in German forestry, thanks to careful provenance research. In his studies of foreign tree species, Langlet (1938) drew attention to the importance of the correct choice of seed origin. This had already been pointed out by Lagerberg (1930) and has also been emphasized by Stefansson (1957), Hagner (1971), Hagner & Fahlroth (1974), Kiellander (1976) among others.

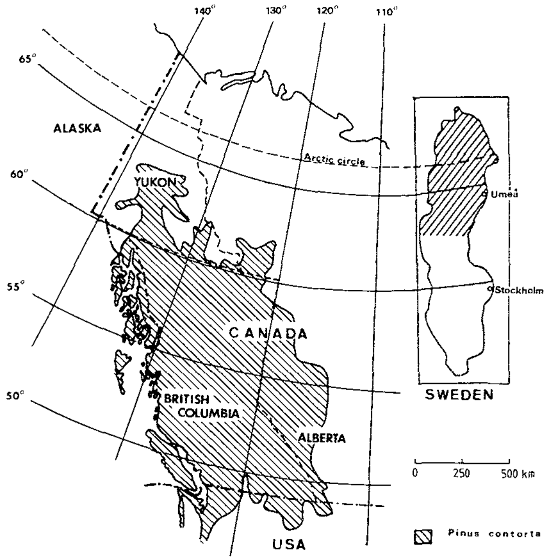


Fig. 1. Occurrence of *Pinus contorta* in its northern range of distribution and investigated area in northern Sweden (for location of trial sites see Karlman, 1984).

Recommendations for a provenance transfer scheme for northern Sweden were drawn up by Hagner & Fahlroth (1974), Remröd (1977), and the Swedish National Board of Forestry (1979). These guidelines have, however, later been revised by Lindgren (in manuscript). The geographic variation of provenances, based on the annual growth rhythm in *Pinus contorta*, was studied by Dietrichson (1970) and Hagner (1970, 1980*a*, 1980*b*).

The prime intention of this study has been to follow, in detail, the development, in nature, of the pathogen—host plant relationships of an introduced tree species and to clarify

1. the ecological importance of parasitic fungi for *Pinus contorta* of different provenances,
2. at which stage of the life-cycle the different kinds of parasitic fungi start causing damage to *Pinus contorta* and

3. which provenances are most resistant to fungal attack and to other kinds of damage.

A continuous check on the occurrence of pathogenic infections of *Pinus contorta* has been considered desirable from a forestry point of view, not least because of what has happened on previous occasions, when tree species have been brought from one continent to another. Fungal attacks on *Pinus contorta* in Fennoscandia have been reported by Kujala (1950), Stefansson (1957), Kaasa (1973), von Weissenberg (1975, 1978), Kiellander (1976), Roll-Hansen (1978) and Karlman (1976, 1979, 1980*a*, 1980*b*, 1982). Martinsson, Karlman & Lundh (1983) studied the mortality rates and degree of damage suffered by both *Pinus sylvestris* and *Pinus contorta* in Sweden 4–9 years after the plantations were established. The primary subject of their investigations, however, was the damage caused to Scots pine, and lodgepole pine is concerned to a limited extent only.

In the present study attention has been concentrated on the pathogens of lodgepole pine. The susceptibility to attack by various pathogens of ca. 100 different provenances of *Pinus contorta* (ca. 25 000 plants) in northern Sweden (Fig. 1) has been studied over periods of three to nine years. Due to the design of trials, only a small number of Scots pine provenances were included.

Material and methods

In 1976, a total of 21 field trials of *Pinus contorta* were selected in the provinces of Västernorrland, Västerbotten and Norrbotten, in collaboration with the Institute for Forest Improvement. Eleven older trials of lodgepole pine of southern provenances were included in the series, although from a present-day viewpoint they are of limited interest. They can, however, be considered as representing a worthwhile introduction to the later stages of the investigations. The remaining sites, comprising provenance trials laid out between the late 1960's and 1974, included a completely new seed sample covering the entire northern range of *P. contorta* in western Canada (Hagner & Fahlroth, 1974). The occurrence of both saprophytic and parasitic fungi on the trees in the trial plots was recorded. The results from all the trials form the basis of a separate report on the fungi (Karlman, in manuscript).

From 1979 onwards, the investigations were concentrated to eight provenance trials laid out by the Institute for Forest Improvement, the Swedish Cellulose Company (SCA) and the Forestry Faculty of the Swedish University of Agricultural Sciences and two smaller-scale trials of my own:

- Three of the trial sites (Ånge, Edsele, Volgsele) form part of the Swedish Cellulose Company's (SCA) trials of *Pinus contorta*, started in 1967. These plantations include 14 different contorta-provenances and 1 *P. sylvestris* provenance, blocks of 64 plants per plot, with 4 replicates. These trials were investigated during the period 1979–1981.
- Two of the trial sites (Stensvattnet and Pausele) form part of the IUFRO series, in which 82 *contorta* provenances have been tried out on single-tree plots distributed at random over the sites. These trials have been studied since 1976.
- Three of the trials (Sävar, Hornmyr, Moskosel) form part of the Institute for Forest Improvement series, started in 1974, with 19 different *contorta* and 4–5 *P. sylvestris* provenances. These trials have been studied since 1976 (Table 1, Fig. 2).
- My own 2 trials were planted in 1975.

The plantations have been investigated annually with respect to different kinds of damage, primarily those caused by parasitic fungi. These, in most cases, attack plants which have already been weakened by some other agent and it is therefore important to know the primary cause of damage. On this account, the trial sites have been inspected on at least two occasions each year—once or more in the spring (at the end of May—beginning of June) to record any damage due to unfavourable weather conditions and to voles—and once again in the autumn (during September) to record any fungal damage and fruit bodies. Weather damage, and that due to voles, is most readily assessed in the spring or early summer, whereas most fungi produce ripe fruiting bodies in September. During the period 1979—81, the Stensvattnet trial was investigated at least three times a year, because mechanical damage from extreme icing conditions had occurred and its effects were followed up (Karlman, 1980, 1982).

Up to and including 1981, samples were collected from all damaged plants. Species determination of fungi in the field most often enables only a provisional estimate of the frequency of fungal damage to be made, and must be supplemented by microscopical study of fruiting bodies and spores at the laboratory. In particular cases pure culturing of the fungi may be necessary for classification. For all the above reasons, samples for later investigation in the laboratory were taken in the field.

Thus each trial plot was thoroughly investigated for occurrence of saprophytic or parasitic fungi. Stems, branches, twigs and needles suspected of harbouring such fungi were examined under a handlens. Fungi collected in the field were studied in fresh condition and notes were made on macroscopic characters, pathological changes of the host plants due to fungal infection or other agents, the number of dead plants, forest vegetation type and tree provenance.

In addition, detailed microscopic (LM) studies of characters such as the type of ascocarpal and pycnidial tissues, the size and shape of asci, ascospores and conidia, were made on freehand sections or squash mounts of fruit-bodies placed in water and later preserved in lactophenol. When making critical studies of some genera the use of various stains and reagents is desirable. For Ascomycetes (especially discomycetes and unitunicate pyrenomycetes) the first stain to be used should usually be iodine (Dennis, 1968) to see if a positive iodine reaction is given. For some species, e.g. members of the genus *Lachnellula*, prior treatment with KOH (10% for ca. 10 min.) is necessary to obtain a positive reaction (Nannfeldt, 1976), but KOH pretreatment was used routinely as a check in accordance with Kohn & Korf (1975). The fungi were also studied under a Scanning Electron Microscope (SEM) and photographed with a photomacrography camera (Karlman, in manuscript).

The degree of damage was assessed on a 4-degree scale, in which grade 1 indicates a slightly damaged plant and grade 4 a dying plant according to Karlman et al. (1982).

Mainly three of the trials will be discussed in this paper, namely those at Moskosel, Hornmyr and Sävar (Fig. 2, Table 2). Results from the remaining trials were evaluated in Karlman (1984, unpublished diss.).

Description of sites

With respect to weather damage the northernmost site in the series, the *Moskosel* trial, is representative. The Moskosel trial was laid out in 1974 on a burnt-over, previously clear-felled area, on a very stony and gravelly moranic soil of good pine forest quality on a

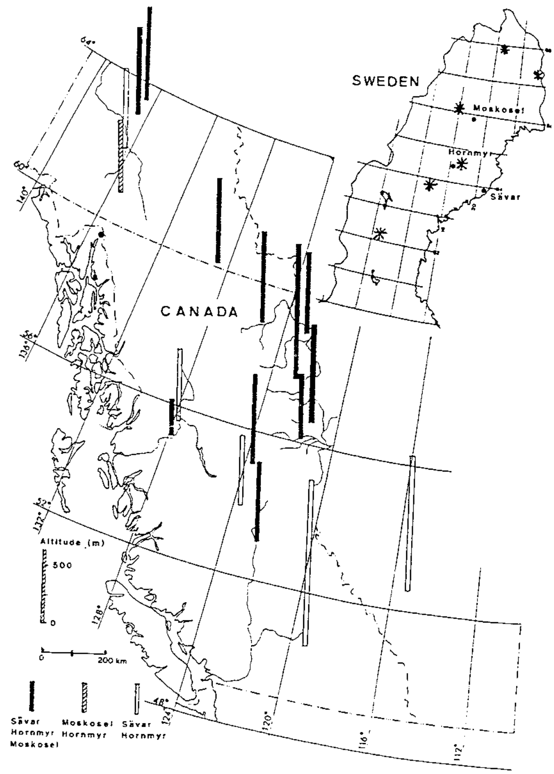


Fig. 2. Map of the origins of the provenances used in the trials at Sävar, Hornmyr and Moskosel in 1974. The provenance localities lie at the bases of the vertical bars, the length of which indicate the altitudes of the provenance localities. Weather stations in Table 3 indicated with *.

north-northeast-facing slope. The vegetation cover is predominantly of *Deschampsia flexuosa* (L.) Trin., *Epilobium angustifolium* L., *Vaccinium myrtillus* L. and *V. vitis idaea* L. The ground surface was first prepared with a TTS-harrow and the plots then planted-up with 1 year-old transplants in paperpots, 2×2 m apart in 20 plots with 4 replicate blocks.

The trial site at Hornmyr lies on a gentle NW-facing slope on a good soil and is bounded in the north by an older stand of Norway spruce (*Picea abies* (L.)Karst. and on all other sides by a grassy Norway spruce plantation of trees now about 75 cm high. The local vegetation is dominated by *Deschampsia flexuosa* (L.)Trin. and the ground is partly littered with twigs and branches. In the centre of the trial site there is a frost pocket. The Hornmyr trial has been regularly inspected for the occurrence of parasitic fungi and other damage, from 1976 onwards, although after 1979 mainly blocks I and III. Vole damage was recorded in 1977/78, 1980/81 and 1981/82 within all four blocks. Results covering survival rates, height increments and tree damage have

Table 1. *Provenances used in the trial at Moskosel*

Origin: Identification no.	Name	Lat. N	Long. W	Alt m	No.
Is 727	Rusty Creek, Yukon	63°30′	136°25′	800	248
Is 728	West Summit Lake, Yukon	63°03′	136°25′	740	256
Is 729	Tantalus Butte, Yukon	62°08′	136°15′	680	256
Is 597	Whitehorse, Yukon	60°52′	135°15′	750	256
Is 730	Watson Lake, Yukon	60°03′	128°43′	725	232
Is 731	2002 Skagway, Alaska	59°27′	135°18′	0–60	256
Is 592	Toad River, B.C.	58°52′	125°21′	760	240
Is 591	Ft. Nelson, B.C.	58°50′	122°42′	460	224
Is 600	Juneau, Alaska	58°25′	134°38′	30	192
Is 732	Trutch Mountain, B.C.	57°40′	122°55′	1150	240
Is 733	Blueberry River, B.C.	56°35′	121°27′	860	208
Is 734	Hudson Hope, B.C.	56°04′	121°53′	530	248
Is 602	Kitwanga, B.C.	55°11′	127°49′	300	64
Is 736	Windy Point, B.C.	55°06′	123°28′	770	64
Is 583	Quesnel, B.C.	53°04′	122°26′	670	48
P. sylvestris					
BD 427	Hortlax (from seed orchard)	65–67°	E	50–450	256
BD 432	Saivo (from natural stand)	68°04′	23°07′+	330	256
BD 429	Saivo (from natural stand)	67–67°45′		300–350	256
BD 428	Saivo (from natural stand)	66°30′		300–350	256

Table 2. *Description of trial sites*

Site	Latitude	Longitude	Altitude m.a.s.l.	Exposition	Number of plants	Number of provenances P.c.	Number of provenances P.s.	Year of planting
Moskosel	65°56′N	19°18′E	400	N-NE	5,120	15	5	1974
Hornmyr	64°25′N	18°23′E	450	NW	6,144	19	4	1974
Sävar	63°53′N	20°33′E	5	–	5,472	18	4	1974

already been published by Rosvall & Strömberg (1980) and by the author (Karlman, 1979, 1982).

The trial site at Sävar was laid out on former cultivated land and the vegetation cover is dominated by *Deschampsia caespitosa* (L.)PB. Damage has been recorded for block I from 1976 to 1981, and for block II from 1979 to 1981. Within all four blocks, any damage due to weather conditions has been recorded from 1980 to 1982.

Climatic background

Climate is generally considered the most important environmental factor determining the distribution and productivity of plants. *Pinus contorta* exhibits an unusually wide ecological amplitude with regard to climate (cf. Karlman 1981). It is one of the most widely distributed species of pine in the world, ranging from Baja California and the southern Rocky Mountains of Colorado and Utah to the Central Yukon Territory, and from sea-level on the Pacific Coast up to 3900 m above sea-level in the Sierra Nevada (Critchfield, 1957, 1966, 1978). In its natural habitats, the lodgepole pine is clearly able to tolerate widely different climatic conditions. Even in British Columbia and the Yukon, the regional climate varies appreciably, depending *inter alia* on site altitude and distance from the coast (see Illingworth, 1971, 1976; Krajina, 1978; Schaefer, 1978 and Nyland, 1980). Since, for Swedish forestry, the most northern provenances of *P. contorta* are those of particular interest, the following description of climate will be restricted to the Yukon Territory.

The climate of the Yukon is more continental than that of northern Sweden, being characterized by long, cold winters and short, warm summers. The annual mean temperature lies below freezing-point (cf. the value for Kiruna in Sweden, Table 3). The mean January temperature is much lower in the Yukon than in northern Sweden. The summer temperatures, however, are almost the same except for a

Table 3. *Mean values for temperature and precipitation in the Yukon (Canada) and in northern Sweden. Table based on 25-year or more data**

	Latitude	Elevation, m	Temperature °C			Precipitation	
			Annual	Jan.	July	Annual	June–August
Yukon weather station							
Watson Lake	60°07′	685	−3	−25	15	434	147
Teslin	60°10′	701	−1	−20	13	326	99
Whitehorse	60°43′	698	−1	−19	14	260	98
Carmacks	62°06′	521	−5	−34	14	247	107
Mayo	63°36′	495	−4	−27	15	293	117
Dawson City	64°04′	324	−5	−29	16	325	140
Swedish weather stations							
Kiruna	67°49′	442	−1.5	−13	13	505	208
Pajala	67°13′	168	−0.1	−13	15	466	181
Arjeplog	66°02′	428	−0.3	−13	14	501	303
Lycksele	64°35′	234	1.8	−12	15	600	237
Junsele	63°42′	210	2.0	−11	15	533	207
Sveg	62°02′	358	2.1	−10	16	558	243

*with the exception of Carmacks. Data from Oswald & Senyk (1977) and from SMHI.

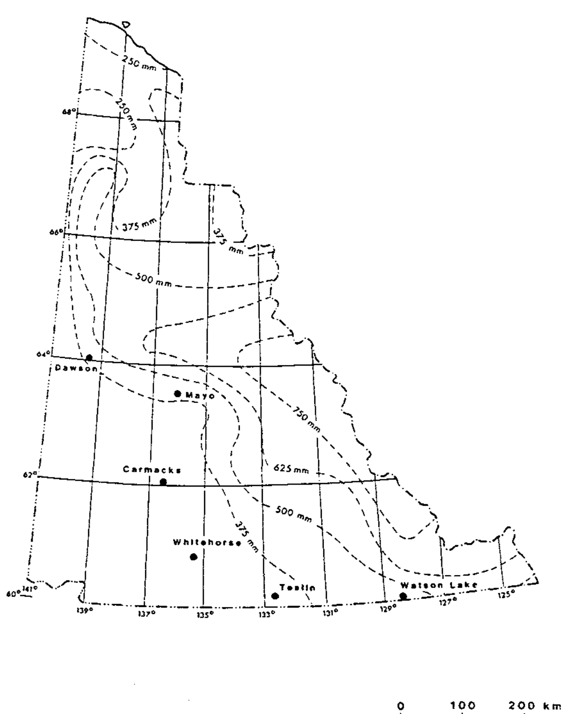


Fig. 3. Isohyets for annual mean precipitation in the Yukon (modified from Oswald & Senyk, 1977).

somewhat higher mean temperature for June in southern and central Yukon as compared with the north of Sweden. The entire Yukon Territory receives a low annual mean precipitation (250–500 mm), though this increases locally with increasing altitude (Fig. 3). The annual mean precipitation in northern Sweden amounts to 400–700 mm, and a greater proportion falls during the growing season than in the Yukon. The growing season lasts about 120 days in the southern Yukon and starts two weeks earlier than in the northernmost parts of Sweden. However, during much of the short growing season, these parts of Sweden enjoy 24 hours of daylight. The hours of daylight in the Yukon at the time of summer solstice range from a maximum of 19 hours in the south to continuous light in the north (Nyland, 1980). Similar daylight conditions prevail in the central parts of northern Norrland (the provinces of Västerbotten and Norrbotten).

The central part of the Yukon was covered by an ice sheet 40000 years ago and again 13000–14000 years ago (Oswald & Senyk, 1977). The southern part of the Yukon was only glaciated during the last Ice Age, whereas the northwestern and western parts were never glaciated. Fennoscandia on the contrary was completely glaciated during the Pleistocene and in the Quaternary glaciations. Permafrost occurs in places within the entire Yukon Territory, varying in depth from a few metres in the south to over 100 m in the north.

The vegetation is discussed in Karlman, 1984.

Weather damage

Results

Weather damage in 1979

Up to 1978 only minor damage was recorded in the provenance trial at Moskosel. At the beginning of June in 1979, however, the northern, but coastal provenances showed signs of severe weather damage. These provenances had nevertheless survived all the winters since they were planted in 1974 (cf. Karlman, 1980). Every tree in the plots of the lodgepole pine provenance Skagway (59°28′) and Juneau (58°25′) was considered to be severely damaged. From the previous year's shoots to the lowest whorl of branches, about 20 cm above ground level, on plants about 0.8 m in height, the needles were dead and reddish coloured (Fig. A, p. 9). When the provenance trial was again investigated, in September of the same year, only 40% of the leading shoots of the plants were found to have died (Fig. 4). The current year's shoots of the remaining 60% had developed normally. Weather damage was also recorded for two of the southern provenances of lodgepole pine at the beginning of June. This was comparatively minor and had affected only the previous year's leading shoots. Within the Kitwanga (55°11′) provenance, the leading shoots of 67% of the plants were found to be dead in September.

The summer of 1978 was colder than normal all over Sweden and the first snow was recorded in central Sweden and in most parts of Norrland already on 24th September (cf. Karlman, 1979, Fig. 1). Cold polar air masses forced their way southwards over the country in the middle of October and by 25th November there was full winter in the greater part of Sweden. According to the Swedish Meteorological and Hydrological Institute (SMHI), December 1978 and January 1979 were the coldest of their respective month recorded since 1860, with previously unrecorded minimum temperatures (Fig. 5). Snow depth, however, was less than normal in the Norrbotten province and in northern Lappland. During January, some very mild days for the season of the year were recorded, interspersed with extremely cold days. From Figure 6 it can be seen that the air temperature during the day on 8th and 9th January lay close to 0°C, with a night temperature of −20°C. The maximum temperature on 20th January was 0.2°C and the minimum temperature −22.4°C, i.e. a diurnal amplitude of 22.6°C. A similar temperature difference prevailed on 19th January. On 27th January the minimum temperature was −41°C, with a snow depth of

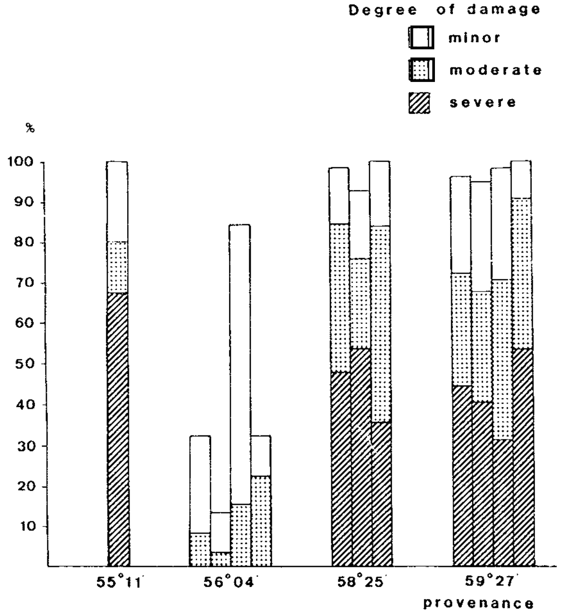


Fig. 4. The frequency of weather damage caused by unfavourable weather conditions during the winter of 1978/79 at Moskosel and recorded in September 1979. The Kitwanga provenance (55°11′N) is represented in one block, the Hudson Hope (56°04′N) in four blocks etc. Number of seedlings: 760.

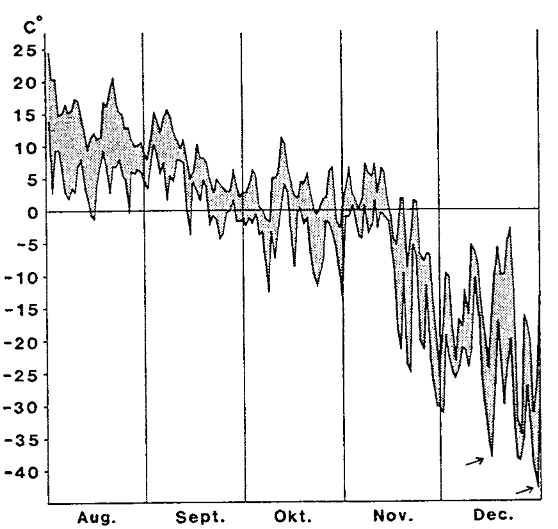


Fig. 5. Maximum and minimum temperature recorded at the weather station of SMHI at Suddesjaur, latitude 65°54′N and longitude 19°06′E at an altitude of 342 m above s.l. August to December 1978. The temperatures at Suddesjaur weather station have been reduced to the actual altitude above sea level at Moskosel. The deviation from monthly mean air temperature for December 1978 was −10.9°C. Arrows indicate temperature extremes.

Fig. A. Severe weather damage within a coastal provenance of lodgepole pine at Moskosel in June 1979.

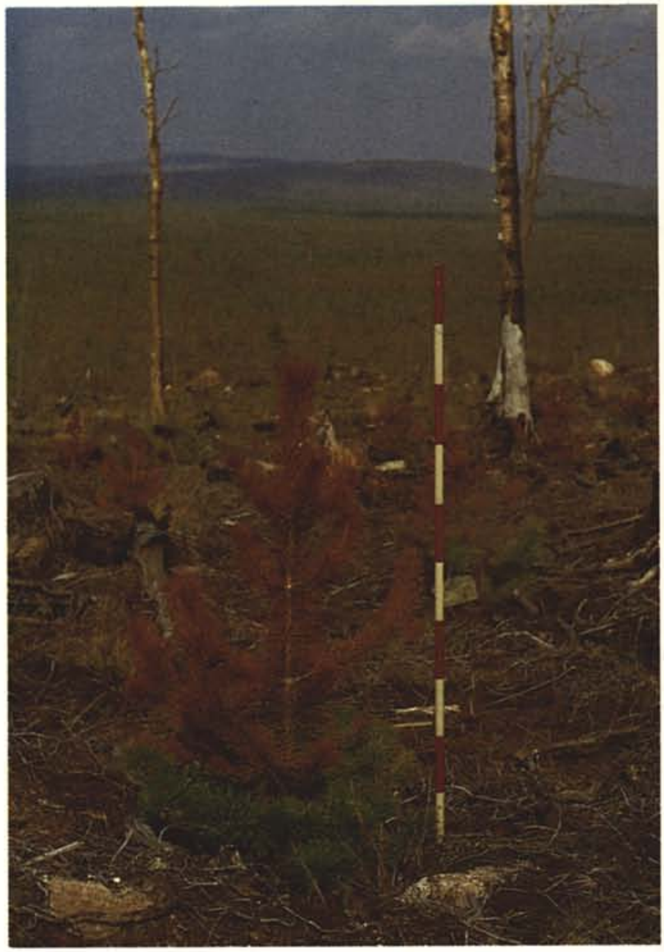


Fig. B. Reddish-brown needles were observed on the SW- and W-facing sides of the plants of southern and coastal provenances of lodgepole pine at Moskosel in June 1980.

Fig. C. A Rusty Creek (63°30′) provenance slightly injured by unfavourable weather conditions during May 1980. Moskosel in June 1980.

Fig. D. Weather damage on a coastal provenance of lodgepole pine at Moskosel in 1981. Those parts of the plants that had been covered by snow during the winter and were exposed to sunshine, due to the vertical shrinkage of the snow-cover during anticyclonic weather conditions in March–April, were less frost-resistant.

Fig. E. Weather damaged needles of lodgepole pine at Moskosel in June 1982, probably due to dehydration in connection with strong NW-winds. The needles had just started to change colour to a lighter yellow at the beginning of June.

Fig. F. Weather damage within a coastal provenance of lodgepole pine. Those parts of the trees which were exposed, due to snowmelt, showed the most serious signs of damage. Sävar in March 1982.

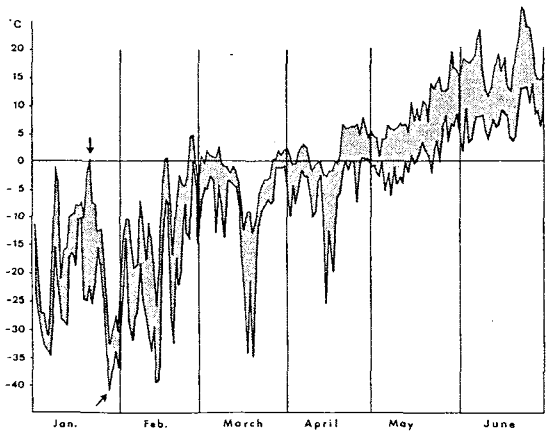


Fig. 6. Maximum and minimum temperature at Moskosel-Suddesjaur January to June 1979. The temperatures at Suddesjaur weather station have been reduced to the actual altitude above s.l. at Moskosel. The deviation from monthly air temperature for January 1979 was −7°C. Arrows indicate temperature extremes, which must have been of importance for the weather damage recorded in May the same year.

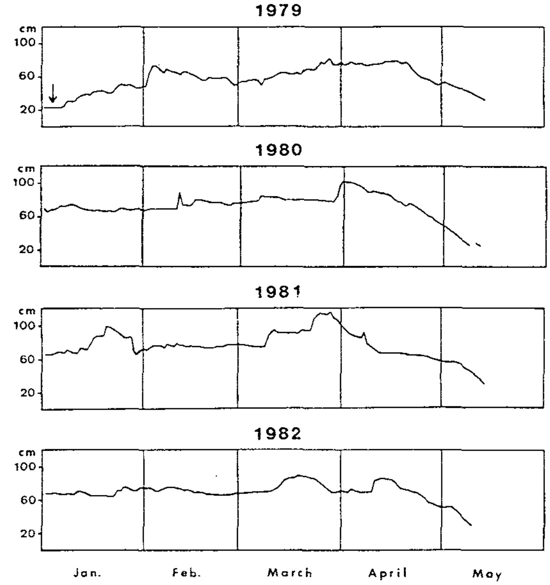


Fig. 7. Snow depth in the Moskosel-Suddesjaur region from January to May 1979–1982. Arrow indicates the exceptionally thin snow-cover in January 1979.

about 40 cm (Fig. 7). In February cold periods predominated. However, on several occasions milder weather occurred, especially at the end of the month. March started and ended with milder weather, with a period of extremely low temperatures about the 20th. Similar fluctuating temperature conditions prevailed during April (Fig. 6).

The data for the depth of snow in the Moskosel-Suddesjaur area between January and May 1979, shown in Figure 7, indicate that the snow cover was only about 20 cm up to 6th January and did not exceed 50 cm until the beginning of February. These values differ markedly from those for the winters of 1980, 1981 and 1982, when, already at the beginning of January, the estimated snow depth in this area was 70 cm. The depth of the snow cover decreased somewhat during February 1979 and at the beginning of March, thereafter increasing once more and then remaining relatively constant until about 20th April. A rapid shrinkage of the snow-cover then occurred during a period of anticyclonic weather conditions.

Minor weather damage to the remaining provenances was also recorded in September 1979 (Karlman, 1984). This probably occurred in the late spring, just before the inspection made at the beginning of June. The maximum and minimum air temperatures on 21st May were +14.5° and −3°C, respectively.

A small number of plants even of the northern provenances were found to be slightly weather-damaged when the second inspection in 1979 was made. The air temperatures did not fall below 0°C throughout June.

Weather damage in 1980

At the end of 1980 a relatively high frequency of weather damage to the northern provenances of lodgepole pine was recorded (cf. Karlman, 1980). The weather conditions in May 1980 (Fig. 8) differed markedly from those in May 1979 (Fig. 6). Almost summer temperatures were recorded from 13th to

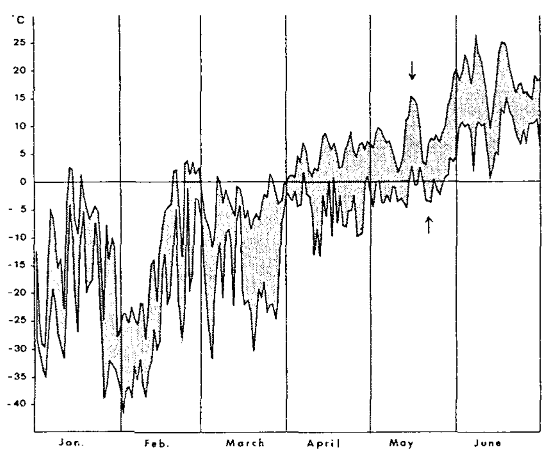


Fig. 8. Maximum and minimum temperature from January to June 1980 in the Moskosel-Suddesjaur area. Arrows indicate temperatures which were of importance for the weather damage recorded in May and September the same year.

16th May. This period was followed by a sudden reversal, when cold polar air masses moved southwards over the country resulting in severe night frosts, which also occurred in southern Sweden.

The provenance trials at Stensvattnet and Hornmyr were inspected both in the middle of May, when no weather damage was recorded, and two weeks later, when reddish-yellow coloured needles were noted on the previous year's shoots of the northern lodgepole pine provenances (Fig. C). Nevertheless, in all cases weather damage caused was considered to have been only slight. The provenance trial at Moskosel was inspected on 30th May and on 18th September. On the latter occasion a higher frequency of weather damage was recorded than in May (Fig. 9). Temperatures below 0°C were not recorded during June.

January, too, was abnormally cold all over Sweden, especially at the end of the month, when extremely cold polar air masses moved southwards over the country. This cold period lasted until 14th February. However, at this time the saplings were protected by a 70 cm-deep snow-cover (Fig. 7). Anticyclonic weather conditions prevailed in March, with strong insolation during the day and low temperatures at night. An influx of mild air from the south at the end of March led to heavy precipitation, in the form of snow, in Norrland. During April the difference in air temperature in the daytime and at night was considerable and the depth of the protective snow-cover diminished rapidly (from over a metre to half a metre by the end of the month). All the lodgepole pine provenances suffered weather damage (Fig. 9), but those of the Scots pine were either unaffected or showed a very low frequency of damage. Saplings on exposed plots in all four blocks showed higher frequencies of damaged needles than the others (cf. Hornmyr trial). Reddish-brown needles were most often observed on the SW and W-facing sides of the plants (Fig. B).

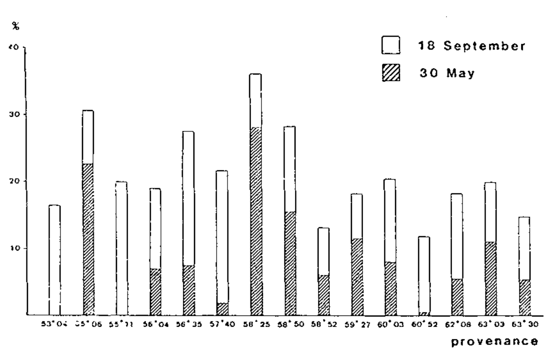


Fig. 9. Weather damage recorded in May and September 1980 at Moskosel. Initially 3824 seedlings of *Pinus contorta.*

Weather damage in 1981

In the spring of 1981 most weather damage was noted for the least hardy provenances. As in 1979, the Skagway (59°27'), the Juneau (58°25') and the Kitwanga (55°11') provenances showed high frequencies of damage. However, dead needles were noted only on the previous year's shoots and on the upper whorls of branches. Those parts of the plants which had been covered by snow were undamaged. (Fig. D).

On several occasions during January, rapid and wide fluctuations between extremely low and fairly high temperatures were recorded (Fig. 10). On 8th January the maximum temperature was +6°C and the minimum temperature −29.8°C, and on 9th January +3.8°C and −8°C, respectively. On 12th January temperatures above 0°C were once again recorded, but on 19th January a record low value of −43.8°C occurred. The end of the month was unusually mild for the time of year. The depth of the snow cover varied from 70 to 100 cm during January. February was characterized by relatively cold and dry weather, March by a rapid succession of cyclones and low air temperatures. The snow depth had increased to 115 cm by the end of the month. Extremely warm weather predominated during the first two weeks in April, with a wide amplitude for the day and night temperatures. Intense solar radiation caused the snow-cover to shrink and by mid April was only as

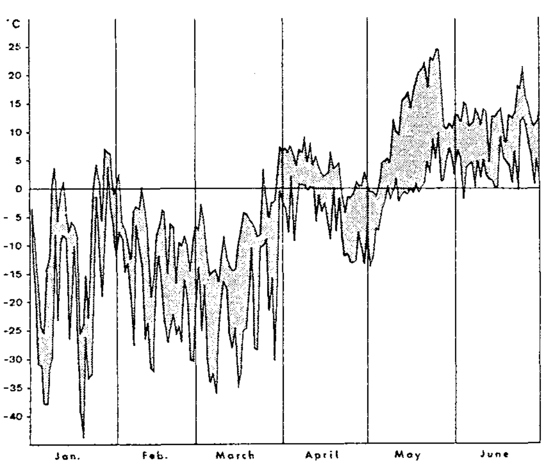


Fig. 10. Maximum and minimum temperature from January to June 1981 in the Moskosel-Suddesjaur area. The temperatures at Suddesjaur have been reduced to the actual altitude above s.l. at Moskosel.

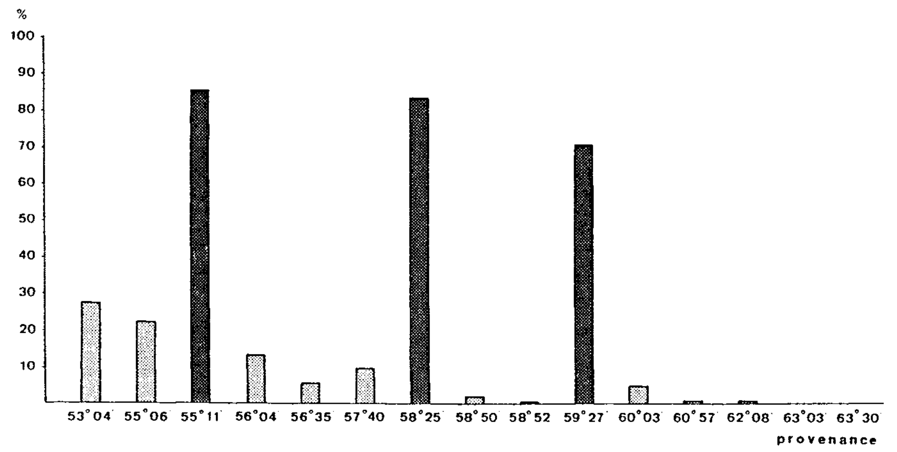


Fig. 11. Weather damage at Moskosel recorded in 1981. Initially 3 824 seedlings of *Pinus contorta.*

deep as it had been in the first week of January (Fig. 7). The prerequisite conditions for the above-mentioned types of weather damage thus occurred in both January and April. May started with temperatures below normal for the time of year; later temperature increased to almost summertime values, breaking previous records. Needles damaged by weather were found on only a few trees of northern provenance (Fig. 11).

Weather damage in 1982

At the beginning of June 1982, unusually high frequencies of weather damage were recorded for all lodgepole pine provenances. For the first time during the entire investigation period, even the provenances of Scots pine suffered from pronounced weather damage. The type of damage, too, differed markedly from that in the preceding years. The damaged needles were completely dehydrated and had only just started to change colour to a lighter yellow (Fig. E), at the time of inspection in the beginning of June. Most of the provenances were only slightly damaged, with the exception of the Skagway, Juneau and more southerly provenances, for which moderate to severe (grades 2 & 3) weather damage was recorded (Fig. 12). A characteristic of the weather damage noted in 1982 was that it was not confined to the leading shoots and the upper whorls of branches. On most trees desiccation damage was also observed on branch whorls somewhat lower down. Weather-damaged needles were in general found on the W and NW-facing sides of the trees. Storm-force winds were

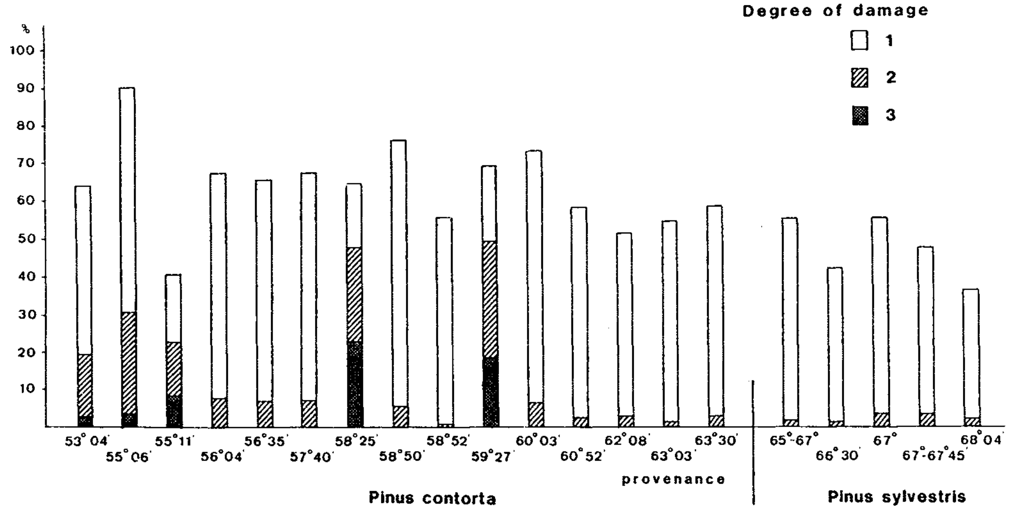


Fig. 12. Weather damage at Moskosel recorded on the 3rd of June 1982. Initially 4 848 seedlings of *Pinus contorta* and *P. sylvestris.*

Table 4. *Wind velocity, in m · sec^{-1}, at SMHI:s weather station at Suddesjaur January–May, 1982 (diurnal mean value)*

Date	Wind velocity	Wind direction
15 January	12	W
16 March	10	W
26 April	10	NW
13 May	10	NW
29 May	10	NW
31 May	12	W

reported by the Swedish Meteorological and Hydrological Institute (SMHI) over a wide area of upper Norrland, both in January and in April 1982. High windspeeds were recorded in the Moskosel-Suddesjaur area not only in January and in April but also in May 1982 (Table 4). For the first time during the entire investigation period relatively high frequencies of tilted trees were also recorded (Fig. 13).

To try to determine the exact time during the late winter and early spring at which weather damage occurs, the Sävar trial was kept under observation from the end of January 1982 until the beginning of June of the same year. No weather damage was observed when investigations started in late January. However, reddish-coloured leading shoots of the southern provenances and coastal provenances of lodgepole pine were observed at the end of March (25/3), following a period of predominantly anticyclonic weather with intense insolation during daytime and low temperatures at night. The needles of those parts of the saplings which had become exposed, due to snow-melt, turned a reddish colour after two weeks (Fig. F). On 7th March the maximum air temperature at Moskosel was +0.8°C and the minimum temperature −12.6°C (Fig. 14). Similar temperature conditions prevailed until the end of the month and throughout April. During May, too, a wide amplitude between the day and night temperature was noted. The diurnal temperature amplitude on 19th May was 15.2°C (+10°C during the day and −5°C during the night). Truly summer temperatures were first recorded at the beginning of June in 1982, but temperatures below 0°C were also recorded later. When the trial was inspected in September 1982, a high frequency of dead reddish-brown coloured needles was observed on trees of all provenances.

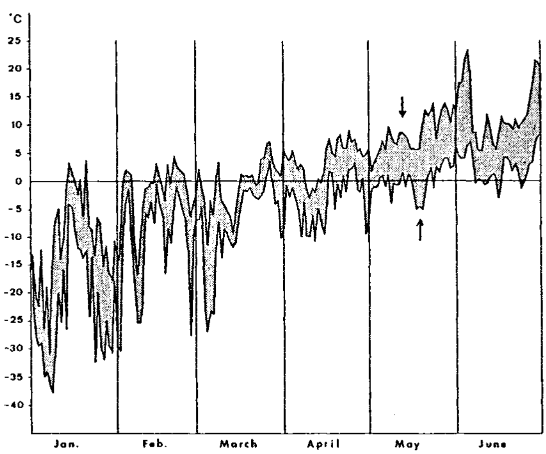


Fig. 14. Maximum and minimum temperature from January to June 1982 in the Moskosel-Suddesjaur area. The temperatures at Suddesjaur have been reduced to the actual altitude above s.l. at Moskosel. Arrows indicate temperatures, which might have been of importance for weather damage recorded in June and September the same year.

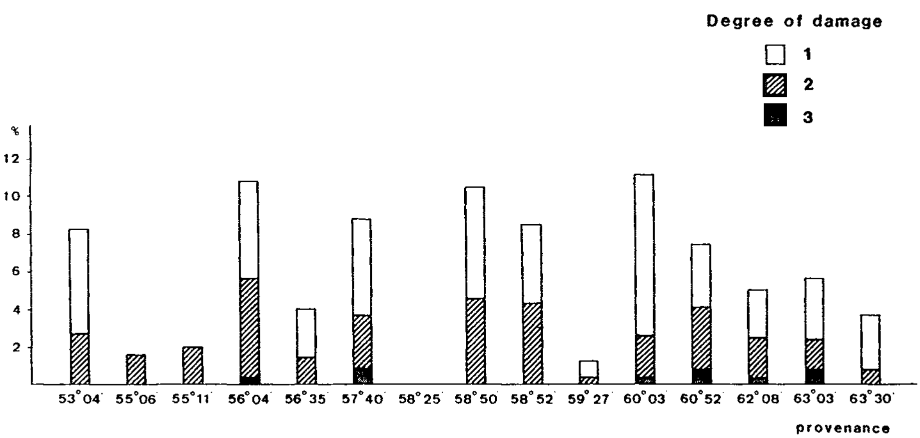


Fig. 13. Frequency of tilted trees at Moskosel in June 1982. Grade 1 = ca. 15°, grade 2 = ca. 15–45° and grade 3 = ca. 45–90°. Initially 3 824 seedlings of *Pinus contorta.*

Discussion

Background

Considering that isolated extreme anomalies in the natural fluctuations of climate may be of decisive importance to the long-term survival of an introduced tree species, there is good reason for making an effort to analyze in detail the types of weather damage recorded within these provenance trials. It may seem to be of little interest to discuss possible weather injuries to the less hardy provenances, but in fact these represent a valuable body of material for a study of the reasons why the more hardy provenances also suffer at times from weather damage. In the case of the latter this is generally less severe, but does reduce the vitality of both seedlings and young trees and thereby increases the risks of infection by secondary pathogens.

Within its natural range in western North America, *Pinus contorta* is subject to a special kind of weather damage called "Red belt". This occurs most frequently in the Canadian Rocky Mountains at an altitude of 1 000–1 500 m above sea level. It causes the death of shoots and needles of the lodgepole pine and other conifers. Sudden oscillations in air temperature during the spring, when cold arctic air in a valley bottom becomes abruptly mixed with warm and dry air carried by the Chinook wind from the Pacific Ocean, are considered to be the main cause of "Red belt" (Mac Hattie, 1963). This particular weather phenomenon is also well-known in Scandinavia (Langlet, 1929; Venn, 1962). "Red belt" has been recorded from Sweden, but is not so frequent here as in Norway, because of the substantial topographical differences between the two countries. Although large areas of Scots pine in northern Sweden were severely damaged during the spring of 1980 (own observations), this type of damage is less important in Sweden than in the natural habitat of lodgepole pine in Canada.

Weather damage as observed in the provenance trials reported here can best be understood in relation to its physiological background. Basic physiological studies usually deal with single factor effects; under field conditions factors do not operate individually but in combination. This must be clearly understood, when the individual effects and mechanisms are described below.

Under natural conditions, conifer seedlings can endure relatively severe cold, providing that the fall in temperature to freezing-point and below occurs slowly. On the other hand, plants suffer from intense climatic stress when exposed to rapid changes in temperature (Weiser, 1970; Levitt, 1978; Christersson, 1980; Venn, 1980). The results of most investigations have shown that frost hardiness increases gradually during the autumn, reaches a maximum during the coldest months, and thereafter decreases during the late winter (Aronsson & Eliasson, 1970; Tranquillini, 1979; Cannell & Sheppard, 1982). The climatic factors which initiate the development of hardiness are a shortening in day-length and low night time temperatures (Vaartaja, 1954; Eiche, 1966; Christersson, 1978). According to Jonsson et al. (1981), the shortening of the photoperiod is the most important factor for *Pinus contorta*. Genetic factors and the supply of nutrients also influence the development of frost hardiness (Aronsson & Eliasson, 1970). Langlet (1936) found a strong correlation between a high dry matter and sugar content of the needles and increased hardiness. Experimental data clearly indicate that the lodgepole pine achieves the same degree of hardiness as the Scots pine with a lower dry matter content of the needles (Jonsson et al., 1981). Simonovitsch et al. (1967) found that RNA- and protein production increased during the hardening-off process.

Physiologists make a distinction between extracellular and intracellular freezing. For plants growing in the temperate zone, extracellular freezing normally occurs during winter (cf. Karlman, 1980) as a result of the gradual fall in air temperature (Levitt, 1978), which usually occurs at a rate of only a few degrees Celsius per hour (Parker, 1955; Weiser, 1970). Ice crystals are formed in the intercellular spaces and the plant cell becomes dehydrated. In laboratory experiments, ice crystal formation can be avoided by very rapid cooling-down and warming-up (Sakai & Yoshida, 1967; Weiser, 1970). During the hardening-off process, the plasma membrane of the cell becomes stabilized so that it is able to tolerate extremely low temperatures. On thawing, the water in the intercellular spaces passes back into the cells once more and they resume their normal physiological functions. During periods of intense and long-lasting cold, dehydration can lead to cell injury, especially to the cells of non-hardy provenances (Levitt, 1978; Tranquillini, 1979). The proteins within the cell membrane change and lose their capacity of absorbing water from the intercellular spaces—i.e. the cell dies (Aronsson & Eliasson, 1970; Asahina, 1978; Christersson, 1980). Intracellular freezing is a result of a rapid cooling and is always fatal for plants (Parker, 1955; Tumanov & Krasavtsev, 1959; Alden & Hermann, 1971). Rapid thawing-out, initiated by intense insolation during the late winter and followed by a rapid fall in temperature (more than 10°C per minute) may result in intracellular freezing (Weiser, 1970; Aronsson & Eliasson, 1970). According to Peace (1962) and Stefansson & Sinko (1967), among others, the most common reason for weather damage during late winter and early spring is physiological drought, brought about by a combination of intense insolation, an increased rate of transpiration and frozen soil.

Examples of interactions between most of these factors may be found in the present material.

Damage during midwinter

Parker (1955), Junghans (1959), Tranquillini (1979) and Cannell & Sheppard (1982) have all shown that the frost hardiness of conifer seedlings is most pronounced during midwinter. However, cold conditions alone have been considered capable of causing damage to plants during severe winters, especially those of non-hardy provenances (Sylvén, 1924; Wagener, 1949; Peace, 1962; Parker, 1963; Wenzel, 1965; Eiche, 1966; Venn, 1970; Levitt, 1978; Tranquillini, 1979; Wardle, 1981). The degree of frost hardiness may vary according to the prevailing temperature conditions. If seedlings are exposed to high temperatures during midwinter, their hardiness decreases and is recovered only insignificantly during a subsequent period of low temperatures (Day & Peace, 1937; Eiche, 1966; Venn, 1970). Seedlings are particularly sensitive when a succession of mild and cold periods occurs (Watt, 1956; Tumanov & Krasavtsev, 1959).

The Moskosel-Suddesjaur area was characterized by that type of weather during January 1979 (Fig. 6). It has been shown that the frequency of thawing and freezing has an influence on the frost hardiness of plants (Langlet, 1929; Levitt, 1956, 1978; Venn, 1980) and the rate of change in air temperature is of the utmost importance for their ability to endure low temperatures (Tranquillini & Holzer, 1958; Tumanov & Krasavtsev, 1959; Wardle, 1981). Sudden changes in temperature are more disastrous for the plants than slow ones. Venn (1980) suggested that air humidity may be of some importance in the occurrence of weather damage. Experiments with Norway spruce seedlings have shown that more severe frost damage occurs in a humid than in a dry atmosphere.

The summer of 1978 was abnormally cold all over Sweden and the autumn was characterized by early and hard frosts. Extremely low temperatures were recorded in the Moskosel-Suddesjaur area in December (Fig. 5). According to several workers (Løfting, 1966; Venn, 1970; Dietrichson, 1970; Holtmeier, 1971; Tranquillini, 1979) a correlation exists between the severity of weather damage and the air temperatures prevailing during the preceding growing season. Kullman (1981), from his studies of high-altitude forest in central Sweden, found that no direct and simple relationship existed between these various factors, but he did not preclude the possibility that below-normal temperatures in summer may represent one of several factors which predispose to weather damage in the following winter and spring. Dietrichson (1964) drew attention to the fact that, in Norway, winters in which severe frost damage was observed, e.g. in 1902/03 and 1907/08, had been preceded by a sequence of warm summers followed by colder ones, with more precipitation than usual and an onset of low air temperatures about −10°C already in September and severe conditions in the following winters (temperatures around −40°C). Similar conditions occurred in both Norway and Sweden in the winter of 1962/63 (Eiche, 1966; Venn, 1970). Dietrichson, however, was of the opinion that several other factors may be important for the occurrence of such frost damage, including the length of the growing season.

The air temperature during the autumn has also been considered important. In his investigations on the hardiness of different species of exotic conifers in Sweden, Sylvén (1924) observed that "early, and hard, autumn frosts, following unfavourable summer conditions with respect to the vegetation" (transl. from Swedish), resulted in a delayed, and insufficient, maturation of the shoots. This had predisposed to frost damage from the extremely low temperatures experienced during the following winters, i.e. in this case the winters of 1915/16 and 1916/17. Andersson (1905), Langlet (1960), Roll-Hansen (1961), Horntvedt & Venn (1978) and Wardle (1981) were of the same opinion. Tranquillini (1979) drew attention to the fact that, after relatively cool summers with a short growing season, the cuticular layer of the needles is incompletely developed, leading to an increase in cuticular transpiration during the late winter and a greater liability for the plants to suffer from weather damage (cf. Holtmeier, 1980). Martin et al. (1978) and Christersson (1978), on the other hand, were of the opinion that after a mild autumn, plants were less hardy in the following winter.

At Moskosel, January 1979 was characterized by alternating mild and cold periods (Fig. 6), which resulted in a loss of hardiness by the *P. contorta* plants. At the turn of the month, severe cold set in, with a protective snow-cover of only 20–40 cm depth. The snow depth which was about 50 cm at the beginning of March 1979, may nevertheless have varied locally. The field trial at Moskosel, which is situated on a NNE-facing slope at the far end of an extensive clear-felled area, is very wind-exposed, i.e. the depth of the snow-cover at Moskosel may well have been less than that recorded in the immediate vicinity of the weather station at Suddesjaur. However, weather damage of the degree reported above was only observed once during the entire investigation period, namely in spring 1979. Most probably, therefore, the most severe damage here must have occurred in January 1979, when the protective snow-cover was about 20 cm and extremely low temperatures occurred after a previous succession of mild periods, during which the hardiness of the plants diminished. It is less likely that the weather damage had occurred during the autumn of 1978, because when examined at the beginning of June the plants were apparently unharmed, except that their needles were a reddish brown colour. No saprophytic fungi, or secondary pathogens, were found when samples of needles were investigated under a stereo-microscope. After autumn frosts, the needles of Sitka spruce (*Picea sitchensis* (Bong.)Carr.) are commonly shed during the early spring (Redfern & Cannell, 1982).

Damage during late winter/early spring

Late winter and early spring damage occurred every year throughout the investigation period among southern provenances of lodgepole pine. The results at Sävar (p. 15) support the conclusions drawn by Tranquillini (1979) from his investigations on *Pinus cembra* L. in the Alps. He found that those parts of the saplings which had been covered by snow for a long period were not as frost-resistant as those which had been continually exposed. When the snow cover diminishes during the early spring, as a result of intense solar radiation and the high albedo of the snow, the internal temperature of the needles may exceed the air temperature by several degrees Celsius (Tranquillini, 1979; Aronsson & Eliasson, 1970). Christersson & Sandstedt (1978) obtained experimental data indicating a difference of as much as 12–15°C. The ice crystals previously formed in the intracellular spaces melt, but immediately re-form when below zero temperatures occur during the night, or when the sun is sheltered by a cloud. Such repeated thawing and freezing of the ice crystals leads to severe stress on the plants (cf. p. 16). According to Bärring (1967), the spruce needles change colour shortly after a night-frost. Venn (1970) reported an interval of a few weeks. In their investigations on Sitka spruce plantations in Scotland, Redfern & Cannell (1982) found that the needles changed colour 10–14 days after being damaged and Cannell & Sheppard (1982) observed that the current year's shoots were killed by an air temperature of −10°C, following the occurrence of higher temperatures in March–April. Experiments made on the same species in a growth chamber indicate that the needles change colour 3–4 weeks after being damaged.

Both Warming (1895) and Day & Peace (1937) considered that the thawing-out period was the most critical. Venn (1980) found that thawing-out Norway spruce seedlings for 4 minutes was enough for severe damage to occur during a subsequent period of low temperatures. Tranquillini (1979) drew attention to the fact that, at the timber line, where, during the spring, the sun-rays only reach the trees relatively late on in the day because of the surrounding high mountains, the frozen needles thawed out very rapidly. However, the water in the intercellular spaces may freeze again very rapidly at sunset (White & Weiser, 1964; Aronsson & Eliasson, 1970). The importance of aspect is illustrated by the trial at Moskosel, which is situated on a NNE-facing slope, bordered on the southwest side by an older stand of Norway spruce. The sun disappears very quickly behind this stand during late winter. On sunny days in winter, White & Weiser (1964) and Weiser (1970) found that the temperature of thawed-out tissues of the evergreen foliage of *Thuja occidentalis* L. fell by 8–10°C per minute when the sun disappeared behind a hill or some other obstruction. Evergreens which had tolerated extremely low temperatures previously during the winter were nevertheless damaged by a fall in temperature to −10°C after a thaw period (cf. Cannell & Sheppard, 1982).

Stefansson & Sinko (1967) showed that, in the short term, intense insolation during periods of anticyclonic weather during the late winter led to a fall in the water content of needles and shoots. During the autumn water content of the needles was over 65% (Stefansson pers. comm., 1983). When the water content had fallen to 47–48% at the end of April–early May, the needles died from dehydration. Those plants which had been covered by snow throughout the late winter had a water content of 60% at the end of April. Stefansson & Sinko (op.cit.) explained the phenomenon of dehydration in physical terms by the so-called "cold wall law, whereby water is drawn towards the cold surface in the evening—nighttime and freezes there. During the daytime thawing occurs and the water evaporates. When the entire plant and the soil are solidly frozen, then little or no compensation for this loss of water can be made from the roots." (translated from Sw.). Such dehydration damage in relation to frozen soil conditions together with intense insolation during the late winter months have also been discussed by Parker (1955), Peace (1962), Sakai (1970), Alden & Herman (1971), Kozlowsky (1976) and Venn (1980). Lindquist et al. (1963), on the other hand, showed that plants of some conifers (*Picea pungens* Engelm.) were more severely damaged when growing in unfrozen than in frozen soil. White & Weiser (1964), from their investigations on *Thuja occidentalis* L. in Minnesota, found that the soil must have been frozen for at least 45–50 days before such dehydration damage occurred. They considered that no relationship existed between the water content of the needles and weather damage. Thawing frost and rainfall were able to make good the water lost by the needles. Wardle (1981) suggested that freezing rather than water stress was the main cause of winter desiccation (cf. Wagener, 1949; Kincaid & Lyons, 1981).

Like Peace (1962) and Sakai (1970), Stefansson & Sinko (1957) stress the role of the cold, dry winds in winter in dehydrating the needles and shoots. Holmgren (1956, 1961, 1963), too, found that wind, in combination with air temperature and snow depth, were the decisive factors influencing such desiccation damage. The occurrence of damage bore some relation to the angle of slope of a site, and thus to the depth of the snow-cover. The snow-cover protected the plants from excessive transpiration. The needles of that side of the plants which faced south-west turned red (cf. Andersson, 1905; White & Weiser, 1964; Wardle, 1981). This observation agrees with my own from the Moskosel trial (Fig. B). According to Pfeiffer (1933), the sides of the plants which are exposed to sunlight are less hardy than the others. A long time elapses before these shoots and branches regain their hardiness following periods of mild weather in the late winter (cf. Sakai, 1966; Venn, 1970; Levitt, 1980; Biryukova & Kharlamova, 1982). Only a few degrees below 0°C are needed before the south or south-west facing sides of the plants become subject to frost damage. The role of wind in this connection is debatable (Tranquillini, 1979; Kullman, 1981; Kincaid & Lyons, 1981; Sowell et al., 1982 and the literature cited therein). It has generally been assumed that strong winds increase the transpiration rate of the needle (Peace, 1962; Satoo, 1962; Sakai, 1970; Kozlowsky, 1976). Wardle (1981), on the contrary, has suggested that strong winds lead to a decrease in transpiration, by lowering the temperature of needles and bringing about stomatal closure. Kincaid & Lyons (1981) accepted that there is some truth in both theories depending on the local conditions.

That *Pinus contorta* is particularly sensitive to the drying-out effect of wind is quite clear (Gail & Long, 1935). In *Pinus contorta* provenance trials in Scotland, those provenances which are normally exposed to wind often suffer severe weather damage. However, coastal provenances do not (Lines, pers.-comm., 1982). They are less sensitive to wind. Lines states that it is the shoots on the windward side of the plants which have red-coloured needles, whilst those on the opposite side are undamaged. As mentioned above, Tranquillini (1979) has shown that the cuticle of the needles does not become fully developed following cool summers, with a shortened growing season, a circumstance which leads to an increased rate of cuticular transpiration during the late winter (see also Holtmeier, 1980 and Wardle, 1974). Holtmeier (1980), in his investigations from the upper timberline in Colorado, obtained indications that westerly winds were an important disposing factor for weather damage. In contrast to Marchand & Chabot (1978), he observed only a few desiccated needles showing signs of mechanical injury.

The Moskosel trial lies as mentioned previously at the far end of a very wind-exposed clear-felled area. Restriction of weather damage to those sides of the plants facing southwest and west, i.e. the sides which had been exposed to temperature fluctuations during the late winter or early spring or both, indicate that, in 1979, wind-exposure played only a minor part. The results obtained in 1982 suggest, however, that winds from the northwest have been of great importance in the occurrence of weather damage (cf. Westergren, 1902; Holmgren, 1956, 1961; Wilson, 1959; Sakai, 1968; Wardle, 1968; Sakai & Otsuka, 1970; Lindsay, 1971; Kozlowski, 1976; Holtmeier, 1980, 1981 and Venn, 1980). In 1982 both Scots pine and lodgepole pine suffered from weather damage. The type of damage differed markedly from that in the preceding years (Fig. E). Relatively high wind speeds were recorded in January, April and May 1982 (Table 4). The high velocity of the wind may have substantially reduced the effective temperature (cf. Wardle, 1981). Damage must have occurred late in spring, as the completely dehydrated needles had just started to change colour to a lighter yellow at the beginning of June. In 1982 damage was localized to those shoots and branches exposed to the strong NW winds. This finding indicates that wind in combination with dehydration and temperatures below 0°C must have been of importance for weather damage in 1982.

The weather damage to the southern provenances, recorded at Moskosel in June 1979, was presumably brought about by temperature oscillations during a period of anticyclonic weather conditions during the late winter months (cf. the provenance trial at Sävar p. 15). Those shoots and branches which thawed out of the snow were less hardy and tended to be more liable to physiological stress and drying out. Weather conditions during March, April were similar in subsequent years. During the winter of 1978 the relatively short (60–70 cm) seedlings of the coastal provenances at Sävar were completely snow-covered during the critical period for weather damage (February to the middle of April). During the late winter period in 1979–1982, the upper whorls of branches melted out of their protective snow-cover during March–April, with resultant damage to the exposed leading shoots in consequence. The snow-cover was very thin all over the Sävar area during the late winter of 1983; only the lowermost whorls of branches were snow-covered, and yet even at the beginning of May no weather damage at all was recorded within this provenance trial, indicating the importance of the snow-cover in this connection. The less hardy provenances of lodgepole pine at Sävar were affected as early as mid-March in 1982. It seems likely that damage to the southern provenances at Moskosel occurred at about the same time of the year as at Sävar (p. 15).

Damage at the time of shoot elongation

Minor weather damage to the remaining provenances in the Moskosel trial in 1979 probably occurred in the late spring, just before the inspection made at the beginning of June. Temperatures below 0°C were recorded on 21st May (Fig. 7). Young conifers are usually very sensitive to temperature changes during the time of shoot elongation. Cannell & Sheppard (1982) found that the new shoots of *Picea sitchensis* were unable to withstand air temperatures below −3 to −5°C during the first few days when they were elongating, until they had attained a length of 3.5 cm. Thereafter they became increasingly hardier.

Both Dietrichson (1970) and, more recently, Jonsson et al. (1981), have shown that the northern *contorta* provenances are more frosthardy than more southern ones. Experiments with *Pinus contorta* plants in a growth chamber indicate that frost-hardiness is closely related to provenance latitude, viz. the further north the hardier. Altitude has also been found important in relation to hardiness "in so far as the populations growing at the highest altitudes were more hardy than those from lower altitudes at the same latitude" (Jonsson et al. 1981). Furthermore Vaartaja (1954) found that coastal races of *Picea sitchensis* and *Pseudotsuga menziesii* had a longer growing period than inland races from the same latitude. The same finding applies also in the case of *Pinus contorta* (Dietrichson, 1970). A clear relationship exists between the length of the growing season and the degree of hardiness (Langlet, 1936).

However, weather damage even to northern provenances of lodgepole pine was recorded in 1980 after a heat-wave in the middle of May followed by a sudden reversal with temperatures below 0°C (Fig. 8). The northern *P. contorta* provenances normally start their growing season earlier than the more southern ones (Hagner & Fahlroth, 1974) and thus were far more sensitive to sudden changes in temperature. A higher frequency of weather damage was recorded in September than in May. This suggests that the damage had occurred during the last two weeks of May and that not all the weather-damaged plants had changed colour at the time of inspection at the end of May. Probably the discolouration of needles occurred a few days afterwards. Even in 1979 a small number of plants of the northern provenances were found to be slightly weather-damaged when the second inspection was made in that year. The air temperature did not fall below 0°C throughout June in 1979 and 1980. In 1982 a relatively high frequency of dehydrated needles was recorded among northern provenances, presumably as a result of hard, dry NW winds during April and May (cf. p. 15).

Summary

The following main types of damage were recorded during the course of the investigation:

1. Severe weather damage suffered by coastal provenances of lodgepole pine during midwinter, after a succession of mild spells followed by a period of extremely low temperatures, which led to intracellular freezing; e.g. the winter of 1978/79.

2. Damage arising in connection with periods of anticyclonic weather during the late winter and early spring, when the snow-cover was in process of melting, with intense insolation during the day, low tem-

peratures at night or when the skies were temporarily clouded over during the day, or both. This repeated thawing and freezing exposes the plants to severe physiological stress. Such weather conditions occurred every spring throughout the investigation period. Frequently the needles on the S and SW-facing branches turned a reddish colour.

3. Damage suffered later on in spring, at the time of shoot extension, a period when the plants are even more sensitive than usual to low temperatures. This type of weather damage was of general occurrence in the spring of 1980 on the plots of the northern lodgepole pine provenances, which start their growth earlier than the more southern provenances.

4. Damage affecting trees exposed to the effects of strong NW winds blowing across the trial site. Shoots and branches on the windward side of these plants exhibited signs of desiccation damage, sometimes with frost damage as well. Wind damage was particularly marked in the spring of 1982, but also occurred in previous years.

5. Physiological drought, due to a high rate of transpiration combined with frozen soil conditions, is yet another factor which is involved in the above-mentioned types of weather damage and which has to be taken into account when considering the risks of weather damage to the evergreen vegetation of the North Temperate Zone.

Weather damage has so far been of minor importance to those provenances well-adapted to their sites. This holds true for all the trials in the series. Up to the winter of 1978/79 even the northern, but coastal, provenances of lodgepole pine were almost unaffected by weather damage all over Sweden. The most severe damage was found in the Moskosel trial. The most important cause of tree mortality among the southern provenances of *Pinus contorta* has been weather injury due to poor winter acclimatization in the nursery, which led to high mortality rates already during the first year after planting (cf. Rosvall-Åhnebrink, 1982).

Parasitic fungi

Results

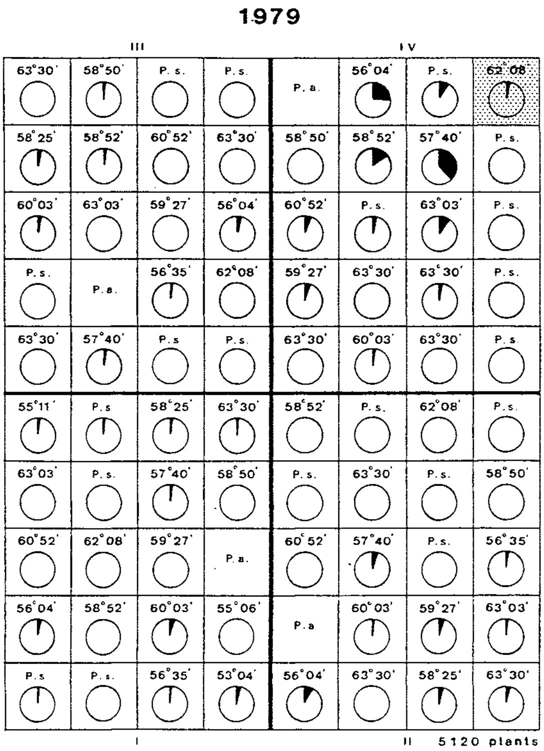
Infection by Phacidium infestans

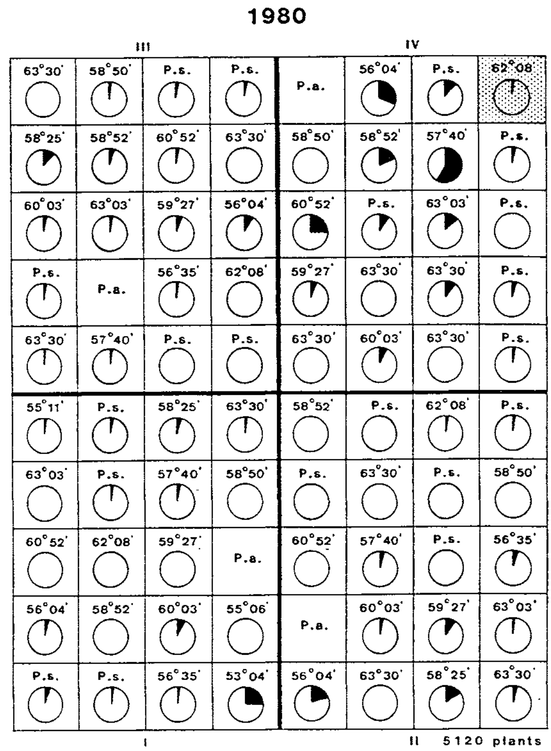
An increase in the frequency of snow blight attack by *Phacidium infestans* Karst. on the northern provenances of lodgepole pine was recorded *in 1979* in the Moskosel trial (cf. Karlman, 1982). The infection spread from some groups of plants in block IV, intended as replacements later (Figs. G, H, p.34). Only a few seedlings of Scots pine were infected in 1979 (Fig. 15). These were situated close to the centre of infection in block IV. The lodgepole pine saplings were attacked first, especially those of the Trutch Mountain (57°40′), Hudson Hope (56°04′), Toad River (58°52′), West Summit Lake (63°03′) and Whitehorse (60°52′) provenances.

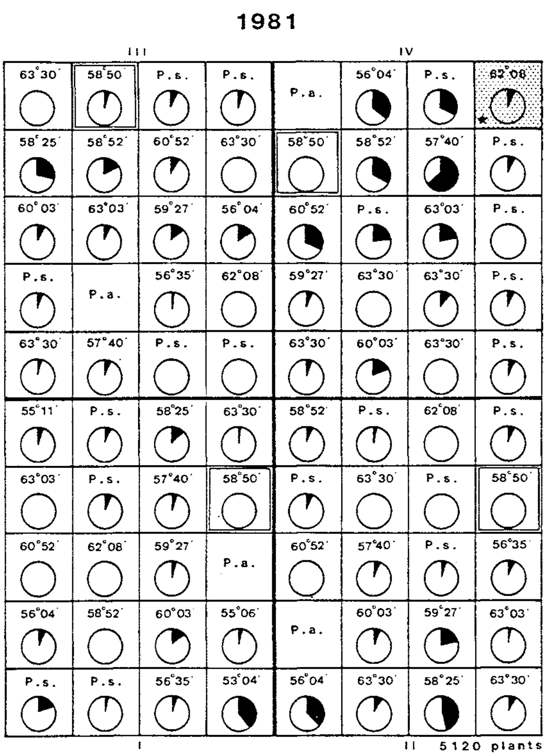
The infection spread further afield *in 1980* (Fig. 16), mainly within block IV. The Scots pine provenances were still only slightly affected. The less hardy lodgepole pine provenances in the margins of blocks I and II showed higher frequencies of damage than did the adjacent provenances. Here the infection spread from naturally regenerated Scots pine outside the field trial site.

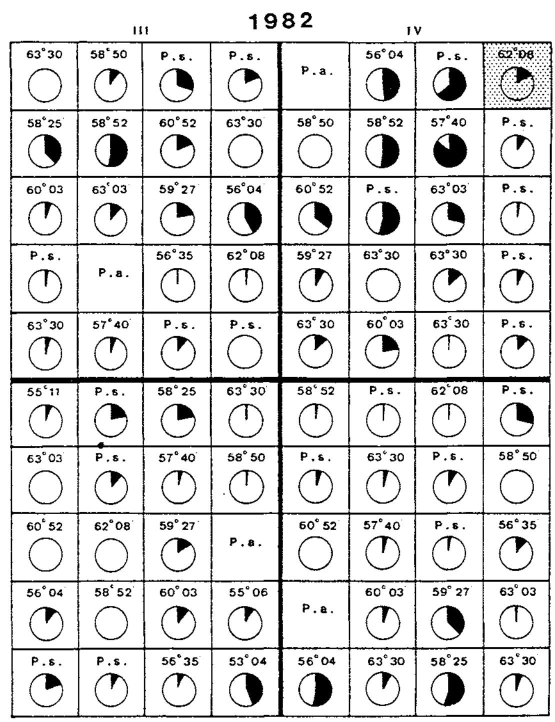
The frequency of snow blight increased markedly *during 1981*, especially on trees of provenances which had suffered severe weather damage during the winter of 1978/79. For the coastal provenance Juneau (58°25′) in block II (Fig. 17), the frequency of attack increased from 3.7% in 1979 to 47.3% in 1981. On four of the twenty plots of Scots pine no infection was recorded. On two plots in block IV, both close to the original centre of infection, the frequency of snow blight attack was ca. 20%, and ca. 10% on one plot in block I. For the remaining Scots pine plots the frequency values lay between 1.6 and 6.4%. The Tantalus Butte (62°08′) *contorta* provenance showed a remarkably low frequency of attack, notwithstanding the fact that the plot in block IV was situated close to the original centre of infection. On the Fort Nelson (58°50′) provenance plots in blocks I, II and IV no snow blight was observed and only minor attacks occurred in block III. Within the plots of the Toad River (58°52′), Whitehorse (60°52′), West Summit Lake (63°03′) and Watson Lake (60°03′) provenances the frequency of snow blight had, however, increased.

The frequency of snow blight also increased within the Scots pine provenances, *in 1982*, although not to









Figs. 15–18. Frequency of snow blight (*Phacidium infestans*) at Moskosel 1979–1982. Infection source marked with line matrix. The origin of latitude of *Pinus contorta* is indicated in the square plots. P.s. = *Pinus sylvestris*, P.a. = *Picea abies*. Every square represents one plot with initially 64 seedlings.

the same degree as on the plots of the most severely attacked provenance of lodgepole pine, viz. Trutch Mountain (57°40′) (Fig. 18). The most northern provenance of lodgepole pine Rusty Creek (63°30′) showed a low frequency of infection, as did the Tantalus Butte (62°08′) provenance. On the other hand, infection rates had increased within the following provenances: West Summit Lake (63°03′) to 27%; Whitehorse (60°52′) 36.2%; Watson Lake (69°03′) 23.7%; and Toad River (58°52′) 53.2%. No attacks were recorded within the plots of the Fort Nelson (58°50′) provenance in blocks II and IV, and only minor attacks within those of the other blocks. From 1982 onwards, the attacks of snow blight on lodgepole pine were considerably less serious. The plants had by then reached a height at which future attacks would be of only minor importance to survival. Grade 2 was predominant (Fig. 19).

In 1983 some trees in all the plots of Scots pine had been attacked by snow blight. Frequencies of 93 and 84% respectively, were recorded for the two plots in block IV situated closest to the centre of infection (Fig. 24). In the autumn of 1983 the majority of the attacks on both lodgepole pine and Scots pine were only of grade 2 severity. The snow blight attacks on the Scots pine saplings in 1984 were, however, more serious.

Severe infection by snow blight was recorded on Scots pine provenances six to seven years after planting at Hornmyr, but only minor infection occurred on lodgepole pine provenances both at Hornmyr and at Stensvattnet (Karlman, 1984).

Weather damage and pathogens

A transplant with reduced vitality is often attacked by secondary pathogens. Thus the frequency of snow blight (*Phacidium infestans*) increased markedly within the plots of the lodgepole pine provenances that had suffered severe weather damage in 1978/79. Ninety-two per cent of the trees of the Juneau (58°25′) coastal provenance in block II had suffered from weather damage, resulting in dead needles from the level of the previous year's leading shoots down to the lowest whorls of branches (cf. p. 8). Up to 1982, 58% of these weather-damaged plants had become infected by snow blight, and 45% of those infected were also attacked by *Scleroderris* canker (*Gremmeniella abietina* (Lagerb.)) Morelet. An additional 16% of weather-damaged plants had been attacked by *Gremmeniella abietina* without being first infected by *Phacidium infestans.* Fifty-four per cent of the trees (29 altogether) suffered *severe* weather damage i.e. no shoots were developed. Of these severely weather-damaged trees 69% (20 trees) were infected by *Phacidium infestans* compared to 34.6% (9 trees) of those not severely damaged. All the saplings that were found to be infected by *Gremmeniella abietina* had been severely weather-damaged in 1978/79. Thirty-eight per cent (8 trees) of the saplings infected by *Gremmeniella* were not infected by *Phacidium infestans* as well.

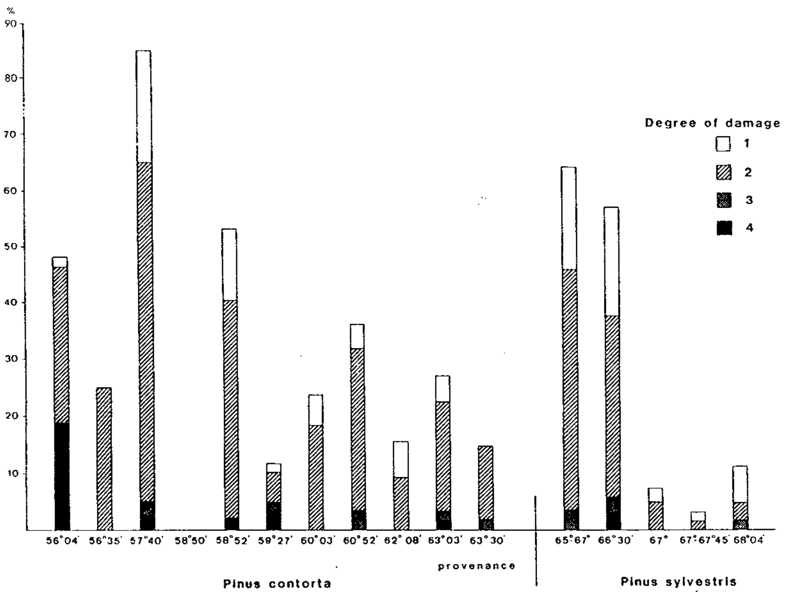


Fig. 19. The frequency of snow blight (*Phacidium infestans*) and degree of damage within block IV at Moskosel in September 1982. Initially 1 216 seedlings of *Pinus contorta* and *P. sylvestris.*

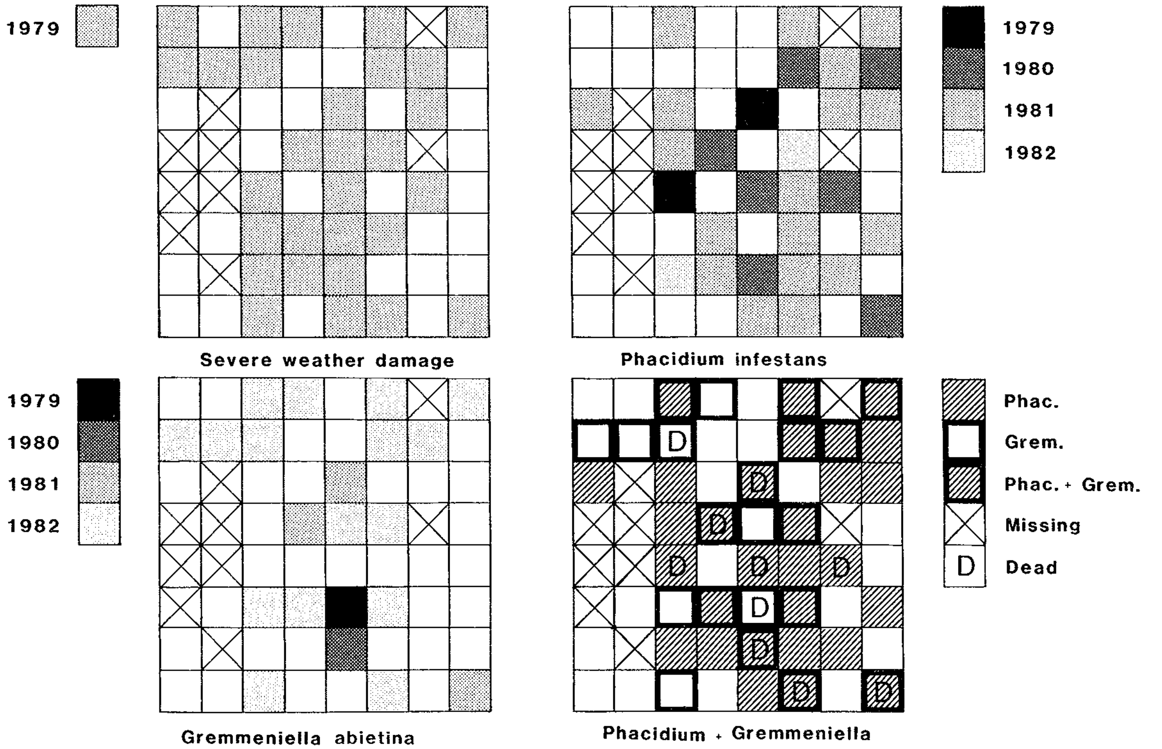


Fig. 20. The frequency of severe weather damage and the spread of *Phacidium infestans* and *Gremmeniella abietina* within a plot of the coastal provenance Juneau (58°25′N) in block II at Moskosel with initially 64 seedlings.

	Ph	$\overline{\text{Ph}}$
SWD	20	9
$\overline{\text{SWD}}$	9	17

$\chi^2_c = 5.18^*$

	G	$\overline{\text{G}}$
SWD	21	8
$\overline{\text{SWD}}$	0	26

$\chi^2_c = 27.47^{***}$

	G	$\overline{\text{G}}$
Ph	13	16
$\overline{\text{Ph}}$	8	18

$\chi^2_c = 0.32^{ns}$

SWD = severe weather damage
Ph = Phacidium infestans
G = Gremmeniella abietina
— = no SWD, Ph, G,

*** : $P < 0.001$
* : $0.05 > P > 0.02$
ns: $0.7 > P > 0.5$

A clear correlation thus existed between severe weather damage and attacks by *Phacidium infestans* for the less hardy lodgepole pine provenances. An even clearer correlation existed between severe weather damage and attacks by *Gremmeniella abietina* (Figs. 20, 21). Within the more hardy provenances of lodgepole pine which had been infected by *Phacidium infestans*, only sporadic attacks by *Gremmeniella abietina* were recorded.

Pycnidia of *Brunchorstia pinea* (Karst.) Höhn were found on the severely weather-damaged plants one or two years after they had been attacked by snow blight. Apothecia of the perfect stage of *Brunchorstia*, *Gremmeniella abietina*, were observed after a further year had elapsed. *Lachnellula flavovirens* (Bres.) Dennis, a species closely related to *Lachnellula pini* (Brunch.) Dennis, was also recorded on needles previously infected by *Phacidium infestans*.

After a *Phacidium*-infected plant has been killed by *Gremmeniella abietina*, its tissues become invaded by

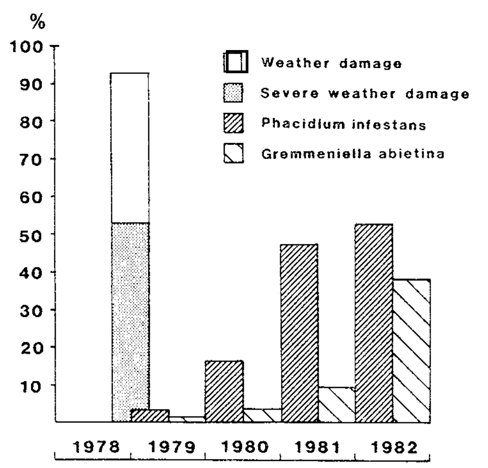


Fig. 21. Severe weather damage and infection by *Phacidium infestans* and *Gremmeniella abietina* 1978–82 within a coastal provenance of lodgepole pine (58°25′N) in block II at Moskosel.

the following saprophytes: *Lophodermium pinastri* (Schrad.: Fr.) Chev., then by *Lachnellula suecica* (de Bary ex Fuck.) Nannf., a saprophytic species which frequently occurs on Scots pine and lodgepole pine in northern Sweden, and finally by *Lophium mytilinum.* (Pers.: Fr.) Fr. On dying plants infected by *Phacidium infestans*, but not by *Gremmeniella abietina, Lachnellula flavovirens* has been recorded, succeeded by *Lachnellula suecica* and after a further year by *Lophium mytilinum.*

Other fungi

Other fungi recorded in the provenance trial at Moskosel were *Sclerophoma pityophila* (Corda) Höhn, *Cenangium ferruginosum* Fr.: Fr., *Tympanis pytia* (Karst.) Karst. with the imperfect stage *Pleurophomella* spp., *Lachnellula subtilissima* (Cooke) Dennis, *Lachnellula pini* (Brunch) Dennis, *Scoleconectria cucurbitula* (Tode: Fr.) Booth with the imperfect stage *Zythiostroma pinastri* (Karst.) Höhn., *Leptostroma pinastri* Desm. (the imperfect stage of *Lophodermium pinastri*), *Mytilidion gemmigenum* Fuck., *Cytospora pinicola* Westd. and *Phacidiopycnis pseudotsugae* (Wils.) Hahn.

Sclerophoma pityophila occurs frequently at the sites of all the lodgepole pine provenance trials in northern Sweden. It was recorded on plants previously damaged by voles, elk, insects, unfavourable weather conditions, and parasitic fungi. *Sclerophoma* is occasionally found as a secondary pathogen, but is usually a completely harmless saprophyte. In the provenance trial at Moskosel, *Sclerophoma* was mainly recorded on weather-damaged plants and following infection by *Gremmeniella abietina.*

Cenangium ferruginosum was recorded together with *Sclerophoma pityophila*, on dead plants of a southern *contorta* provenance (Kitwanga 55°11′) *Tympanis pitya* on plants already infected by *Phacidium infestans, Pleurophomella* spp. on a few weather-damaged plants within the plots of the Trutch Mountain provenance (57°40′), *Zythiostroma pinastri* on the scars caused by previous weather damage, *Leptostroma pinastri*, together with *Lophodermium pinastri*, on plants previously infected by *Phacidium infestans* in addition to *Lophium mytilinum* and the closely-related genus *Mytilidion gemmigenum.*

Minor attacks of *Lachnellula subtilissima* were observed on the Whitehorse (60°52′) provenance plots; *Cytospora pinastri* on dead plants on the Rusty Creek (63°30′) provenance; and finally *Phacidiopycnis pseudotsugae* on lodgepole pine damaged by elk.

Vole damage as a predisposing factor

During the investigation period two of ten trials in the study series were attacked by voles, namely those of Hornmyr and Pausele in the province of Västerbotten. Severe infection by *Gremmeniella abietina* was recorded at Hornmyr two to three years after the vole peak during the winter of 1977/78 (Fig. 22). The most serious fungal attacks in 1982 were recorded for the local provenance of Scots pine (*Pinus sylvestris*) and for the lodgepole pine provenance Whitehorse (60°52′). Fungal attack occurred solely in connection with vole damage caused in 1977/78. Sporadic attacks of *Bruchorstia pinea* were recorded for the southern contorta provenances in the autumn of 1977. Apothecia of *Gremmeniella abietina* were first noted in 1978, on a Scots pine seedling which had been browsed by elk. *Lophodermium pinastri, Leptostroma pinastri, Sclerophoma pityophila* and *Lachnellula suecica* were also recorded on the same plant. *Sclerophoma pityophila* was very frequent on vole-damaged plants and also occurred on those suffering from weather damage. The first *Gremmeniella* attacks were noted on vole-damaged plants in 1979, within the plots of the Whitehorse (60°52′) and West Summit Lake (63°03′) amongst others. The number of plants attacked by *Gremmeniella* increased during 1980 and 1981, especially those of the Whitehorse provenance in block III.

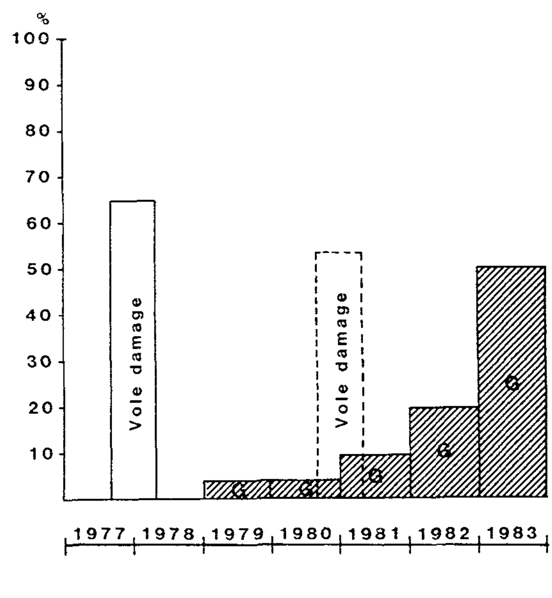


Fig. 22. Infection by *Gremmeniella abietina* following vole damage during the winter of 1977/78 within the Whitehorse provenance plots in blocks I and III at Hornmyr in 1983. Initially 128 seedlings.

By 1983 infection had spread further and plants of all provenances showed signs of more or less serious attack by *Gremmeniella abietina*, although even in that year the most serious damage was recorded for the Whitehorse provenance (60°52′) with 50% of the plants being attacked in block I and III (Fig. 30). Even those of the most northern provenances showed signs of infection. The Watson Lake provenance (60°03′), on the other hand, showed a relatively low frequency of *Gremmeniella* infection, due to the fact that it had suffered a relatively high frequency of lethal damage from voles (grade 4) in the winter of 1980/81.

In addition to *Brunchorstia pinea* and *Gremmeniella abietina, Sclerophoma pityophila, Zythiostroma pinastri, Lachnellula suecica* and *Lophium mytilinum* were recorded on plants damaged in the first instance by vole attacks, the two last-mentioned species from dead tissues. *Lophodermium pinastri,* like sporadic attacks of the honey fungus, *Armillaria* sp. and the northern pine canker, *Lachnellula pini*, were recorded from vole-damaged trees.

During 1984 the infection by *Gremmeniella abietina* was more severe. Even trees that had not been attacked by voles were infected by *Gremmeniella.* Up to 1984 the Tantalus Butte (62°08′) provenance was the provenance least affected by voles. During 1984 even this provenance was infected by *Gremmeniella abietina*.

Height growth in relation to infection by pathogens

The height of all plants in the Moskosel trial was measured in September 1983. Nine years after planting the tallest trees were recorded, within block IV, for the Whitehorse (60°52′) and Trutch Mountain (57°40′) provenances (Fig. 23). The values for these two provenances were also high in block III, but considerably lower within the other two blocks. This indicates that plant height depends not only on the origin of the seed but also on the microhabitat and microclimate—and of course on genetic factors.

Within block III, the Toad River (58°52′) and Watson Lake (60°03′) provenances showed great mean values, the former despite a high frequency of *Phacidium infestans* attack (cf. Fig. 24). The mean height value for the most northern lodgepole pine provenance, Rusty Creek (63°30′), was high in both blocks III and IV. Consistently lower mean height were recorded for the plots that had been replanted with the Rusty Creek provenance, because these plants were considerably smaller when planted out, owing to the use of a different planting procedure in the

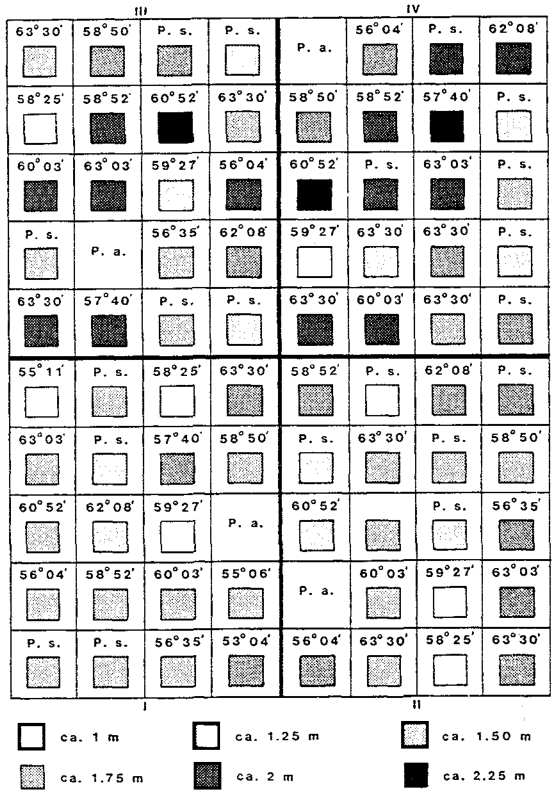


Fig. 23. Mean height values for the different provenances of *Pinus contorta* and *P. sylvestris* at Moskosel recorded in September 1983. Initially 5 120 seedlings.

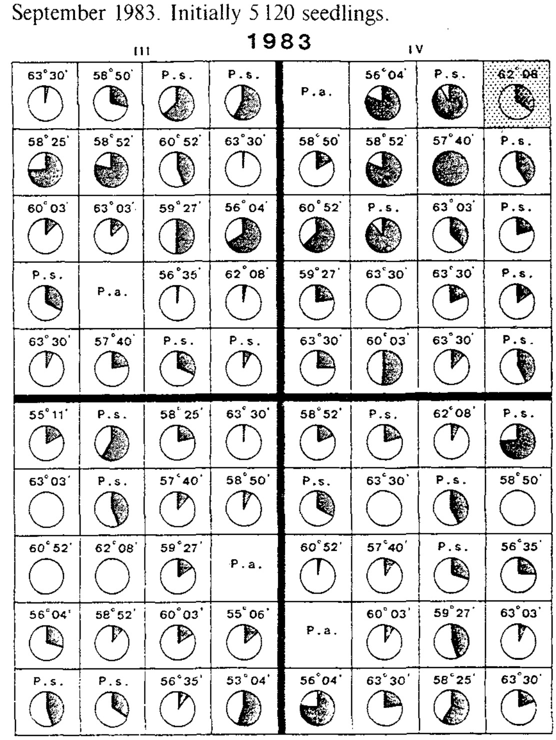


Fig. 24. The frequency of snow blight (*Phacidium infestans*) at Moskosel 1983. Initially 5 120 seedlings.

nursery. The values for the Tantalus Butte provenance (62°08′) were much higher in block IV compared to blocks I—III (Table 5).

No great difference in the growth in height of *Pinus sylvestris* compared to *Pinus contorta* was observed within block I. Scots pine was most productive in block IV, where the mean heights recorded for two of the provenances (66°30′ and 65–67°) were almost as great as the values for the adjacent lodgepole pine provenances, notwithstanding the fact that for just these two provenances of Scots pine the frequency of *Phacidium infestans* attack was increasing. In the remaining three blocks growth in height of lodgepole pine was superior to that of Scots pine.

In a few cases, considerable height differences were noted for the trees within a single plot, depending on the moisture conditions of the site. On level, wet ground occupied by *Sphagnum* and *Polytrichum* species, tree heights were lower than on the drier slopes, where the dominant species, besides *Polytrichum* sp. are *Vaccinium myrtillus* L., *Empetrum nigrum* L. and *Vaccinium vitis idaea* L. When the results shown in Fig. 23 and Fig. 24 are compared it is evident that provenances with the highest frequencies of snow blight, *Phacidium infestans*, were those for which the greatest mean height values were noted, i.e. the Trutch Mountain (57°40′) and the Whitehorse (60°52′) provenances in block IV. Those provenances of Scots pine which were first infected by snow blight were those showing the greatest height growth. Fig. 25 shows that plants which had escaped infection by *Phacidium infestans* had a lower mean height than those which had been slightly attacked by snow blight (grades 1 and 2). Not until more than 50% of the needles were infected (grade 3), was the mean height reduced. The results are quite unequivocal and apply to all the contorta provenances (Fig. 26). A similar trend was discernible for the Scots pine provenances. The mean height for coastal provenances of lodgepole pine was low as a result of severe weather damage and infection by *Gremmeniella abietina*.

Table 5. *Mean height for different provenances of P. contorta and P. sylvestris 9 years after planting*

Provenance	Blocks				
	I	II	III	IV	M
P. contorta					
63°30′	165.0	175.4	203.2	195.5	178.9
63°03′	152.4	184.8	188.4	211.7	184.7
62°08′	116.0	165.0	165.0	206.0	164.0
60°52′	148.6	135.8	230.9	233.2	186.6
60°03′	151.1	157.9	202.4	206.0	176.5
58°52′	153.1	183.9	211.4	204.8	187.4
58°50′	152.3	160.3	172.0	182.7	164.7
57°40′	175.1	158.1	195.3	233.0	186.1
63°30′R					153.8
P. sylvestris					
68°04′	157.3	135.4	141.1	176.1	152.6
67–67°45′	139.3	131.7	164.3	138.0	143.3
67°	–	105.2	121.3	126.7 132.5	131.9
66°30′	162.8	165.7	133.8	209.2	168.0
65–67°	137.8	162.2	138.6	203.2	160.4

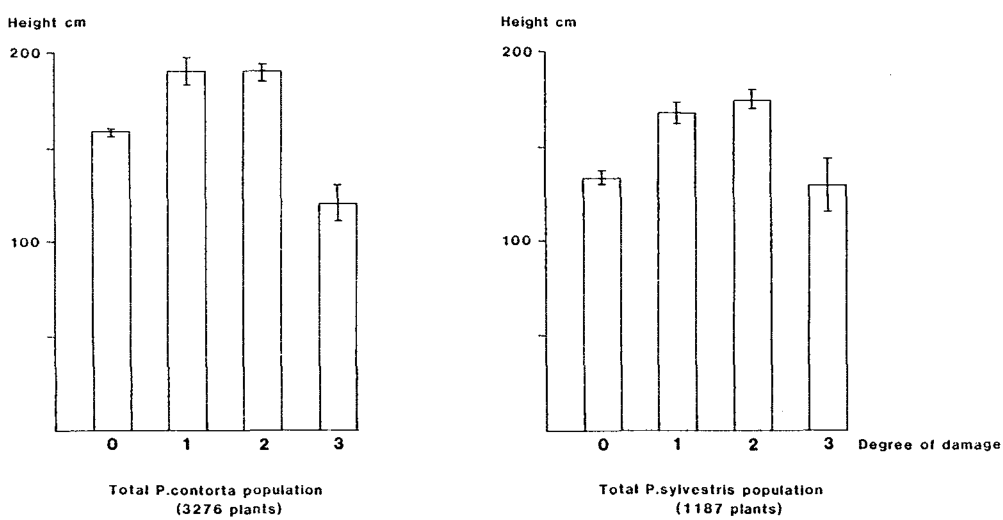


Fig. 25. Mean heights of *Pinus contorta* and *P. sylvestris* in relation to the degree of damage caused by *Phacidium infestans*. Vertical bars represent 95% confidence intervals.

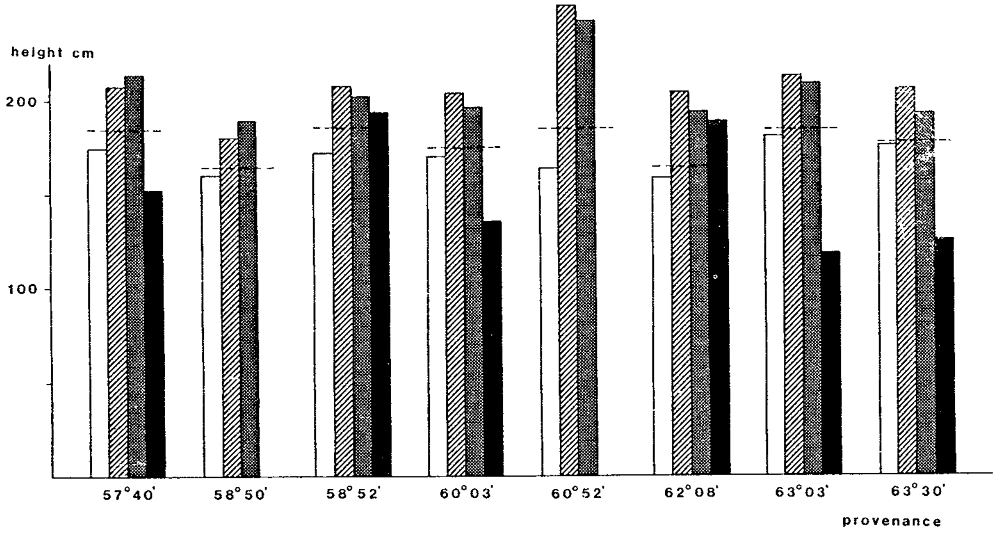


Fig. 26. The correlation between mean height and degree of damage after infection by *Phacidium infestans* for the more northernly provenances of *Pinus contorta* at Moskosel in September 1983 (for the more southernly provenances, see Karlman, 1984). Initially 1 952 seedlings.

Survival

The survival of the trees on the northernmost site (Moskosel) nine years after planting (Fig. 27) was remarkably high. In the autumn of 1983, the Rusty Creek (63°30′), the Watson Lake (60°03′), the Toad River (58°52′), the Fort Nelson (58°50′) and the West Summit Lake (63°03′) lodgepole pine provenances showed the highest survival rates, although the southern provenances had also survived relatively well. The Windy Point provenance (55°06′), however, was only represented in block I, i.e. a total of only 64 seedlings compared to 256 seedlings of the other provenances. The greatest mean heights were recorded for the following provenances: Toad River (58°52′), Whitehorse (60°52′), West Summit Lake (63°03′) and Rusty Creek (63°30′), which were also those with the highest survival rates (Fig. 28). Among provenances that were severely weather-damaged during the winter of 1978/79, mortality had increased, due to secondary infection by snow blight (*Phacidium infestans*) and by *Scleroderris* canker (*Gremmeniella abietina*). The trees of the Trutch Mountain (57°40′) provenance had made good growth in height despite a high frequency of snow blight. For most of the lodgepole and Scots pine provenances, mortality was more pronounced during the initial five years after planting than in the subsequent four years (Fig. 29). The result was similar in the Hornmyr trial (Fig. 30).

Discussion

Background

As an ecologist and forest pathologist I have found it essential to point out the risk factors associated with the introduction of exotic tree species with the intention of making the planting of *Pinus contorta* in Sweden as safe as possible. We possess a well documented knowledge of the parasitic fungi which infect the indigenous Scots pine, *Pinus sylvestris*. Pathogens and other threats to *Pinus contorta* have been studied by the author since 1976. However, this represents a

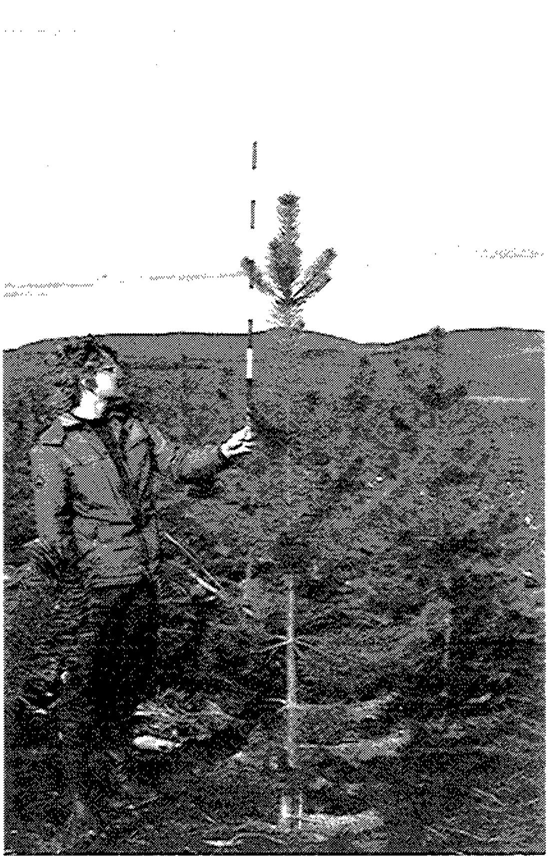


Fig. 27. Phacidium infestans infects the most productive trees. A diminution in growth follows, however. Moskosel in September 1983.

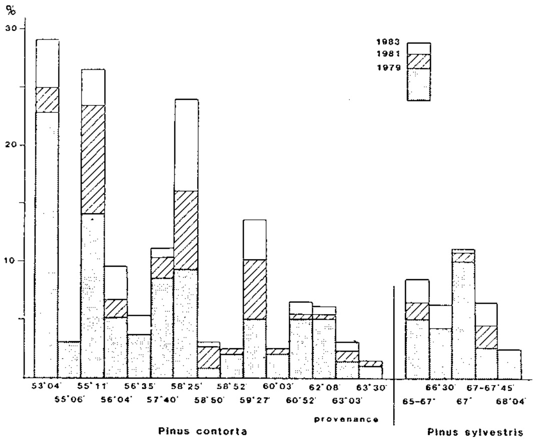


Fig. 29. Mortality rates 5, 7 and 9 years after planting recorded at Moskosel in September 1983. Initially 4 848 seedlings.

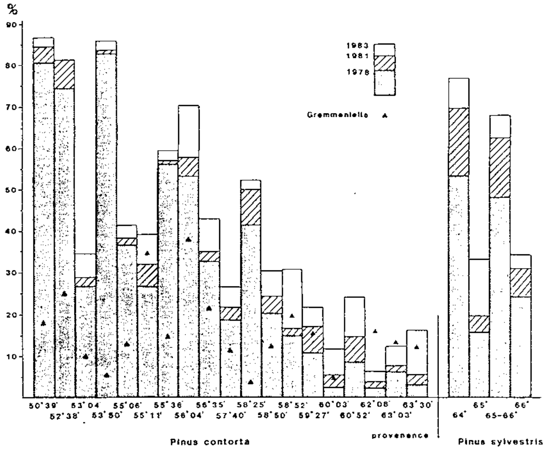


Fig. 30. Mortality rates 5, 7 and 9 years after planting (in 1974) recorded at Hornmyr in September 1983 within blocks I and III (initially 3 072 seedlings). The frequency of *Gremmeniella abietina* is indicated with a ▲.

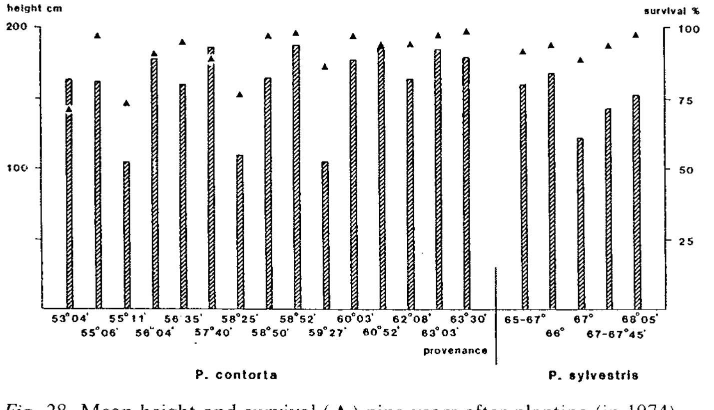


Fig. 28. Mean height and survival (▲) nine years after planting (in 1974). Moskosel in September 1983. Initially 4 848 seedlings of *Pinus contorta* and *P. sylvestris.*

very short space of time compared to the rotation of a conifer (cf. von Weissenberg, 1982). *Pinus contorta* is in addition an exotic tree species which possesses no natural resistance to the specific pathogens found in Scandinavia, which may prove more virulent to a new host not yet adapted to its new environment. Furthermore, any pathogens which may inadvertently be introduced into Scandinavia from the natural habitat of *Pinus contorta* in western Canada could present a potential threat to both the lodgepole pine and the Scots pine in Sweden and thus to Swedish forestry. The threat of internationally dangerous forest tree diseases has already been discussed by the author (Karlman, 1981), e.g. the disastrous epidemics on *Pinus strobus* during the 19th century, the Dutch elm disease, the chestnut blight and the severe pathogens on the Douglas fir in the 1920's. There has been much to learn from these early mistakes in forest practice. The risk of a catastrophe such as that affecting *Pinus strobus*, however, has been reduced considerably by increasing knowledge about correct choice of provenance. All exotics are not foredoomed to fail. Some have actually proved to be of great economic importance e.g. *Pinus radiata* and members of the genus *Eucalyptus*.

As regards the native species of parasitic fungi in Scandinavia, *Pinus contorta* has so far been attacked by the same species as *Pinus sylvestris*, with the exception of *Melampsora* rust (*Melampsora pinitorqua*) and *Lophodermella* needle cast (*Lophodermella sulcigena*), two fungi which occur in Sweden at regular intervals, with a gap of several years' duration between epidemic attacks. Serious infections were recorded on Scots pine in northern Sweden 1979–1981. Hitherto lodgepole pine has been resistant to *Melampsora* rust (cf. Annila et al., 1983), although some susceptibility has been recorded in inoculation trials. Scattered groups of aecidia were observed by the author on lodgepole pine in central Norrland in 1982 (Martinsson, Karlman & Lundh, 1983).

Infection by Phacidium infestans

Snow blight (*Phacidium infestans*) causes severe damage in regenerations of Scots pine in northern Sweden (Björkman, 1948; Eiche, 1966; Stefansson & Sinko, 1967; Langlet, 1968; Martinsson, Karlman & Lundh, 1983). *Pinus contorta* has previously been considered to be relatively resistant to this pathogen. Primarily, trees of southern provenances have been infected (Aldén, 1980; Karlman, 1980*a*). In the Moskosel trial an increase in the frequency of snow blight attack on the northern provenances of lodgepole pine was recorded in 1979 (cf. Karlman, 1982).

However, infection by snow blight is of less importance to lodgepole pine than to Scots pine, due to the former's more rapid growth during the early stages. It is noteworthy that seedlings of Scots pine were infected 1–3 years after those of lodgepole pine, when exposed to the same source of infection (Figs. 15–18). The most productive plants and trees of both *Pinus contorta* and *Pinus sylvestris* were attacked by *Phacidium infestans* (Fig. 25). The mean height for the Scots pine provenances in the autumn of 1979 was lower than that of the lodgepole pine provenances. The needles of Scots pine were relatively short and the foliage was quite sparse. *Phacidium infestans* attacked, in the first instance, the healthiest plants in block IV, those with well-developed and dense needles, i.e. the *Pinus contorta* plants. The *Pinus sylvestris* plants were not infected. In 1980 sporadic, mild attacks of snow blight were observed on the Scots pine provenances, but not until 1982 did two plots of Scots pine in block IV, situated close to the centre of infection, show equivalent values of infection frequency equal to those of the adjacent plots of the lodgepole pine provenances. Those provenances of Scots pine which were first infected by snow blight were those showing the best growth in height.

This finding is in agreement with previous observations made in the field. Björkman (1963) found that the resistance of poorly developed plants in stands of lichen-rich pine forest in northern Sweden possessed a greater resistance to *Phacidium infestans* than more productive plants of the same provenances. Needle anatomy, especially the thickness of the cuticle layer, was considered to be important in this respect. Also Roll-Hansen (1975) observed that dwarfed pines with short needles and a sparse foliage were highly resistant to snow blight attack. Similar observations have been reported by a number of Russian research workers (see Roll-Hansen, 1975 and the literature cited therein). The nature of the snow-cover may have had some part in determining the course of the spread of snow blight in the Moskosel trial. We know from the results of Björkman's investigations (1948), that the spread of snow blight is directly proportional to the depth of the snow cover and that the optimal temperature for the fungus is +15°C, it spreads well at +5°C, and is still capable of spreading to some extent at a temperature of −5°C. Mycelial development is furthered by a cover of loose snow and hampered by dense snow, which provides no real protection against low temperatures. The snow-cover was probably fairly loose and the conditions were thus more favourable for the development of *Phacidium infestans* under the bushy *contorta* saplings than under the relatively small and short-needled saplings of Scots pine. In addition the more bushy branches of lodgepole pine were more easily hit by the spores of *Phacidium infestans* than the short and sparse needles of Scots pine. Whithin the remaining blocks the frequency of snow blight was low in 1979. As mentioned above, the depth of the snow-cover was only 20 cm until well into January 1979. In other words, the prerequisites for a more widespread epidemic of snow blight were not fulfilled in that year.

Factors, contributing to the early attack by *Phacidium infestans* on the *contorta* provenances, may have been the spread of infection from infected *contorta* plants and the very sparse occurrence of snow blight on Scots pine growing outside the provenance trial site. The clearfelled site had been burnt over before seedlings were planted. Before it was clearfelled, in the beginning of the 1970's, the predominant tree had been spruce (*Picea abies*). Zuralev (1960) showed that, in naturally regenerated stands of *Pinus sylvestris*, the plants suffer no attacks of snow blight before they have reached an age of 3–4 years. This probably explains why the frequency of snow blight increased slightly later on (in 1981) on the plots situated on the margins of blocks I and II than on those in blocks IV, where a source of infection was present within the site itself at an early stage of the provenance trial. Furthermore, the weather damage suffered by the *contorta* plants in the plots of blocks I and II would have increased their susceptibility to infection by snow blight (cf. Kullman, 1983).

Weather damage as a predisposing factor to infection by pathogens

Severe weather damage is a predisposing factor to infection by *Scleroderris* canker and *Brunchorstia* dieback (*Gremmeniella abietina*). There is also a minor correlation between severe weather damage and *Phacidium infestans* infection, especially in high altitude stands in northern Sweden. So far, however, severe weather damage has mainly been recorded within the southern and coastal provenances of lodgepole pine. There is a clear tendency, on the more southern sites in northern Sweden, for the severity of attacks by both *Gremmeniella abietina* and *Phacidium infestans* to decrease with increasing latitude and altitude of provenance origin. The observed data well agree with other observations made in Europe and in North America.

A relationship has been documented between already weakened lodgepole pine planted at a high altitude and attacks by *Gremmeniella abietina* (Stefansson, 1957; Roll-Hansen, 1972). A relationship also exists between infection by this pathogen and tree provenances which are not suited to the ecological conditions of the locality, e.g. too southern a provenance (Kohh, 1964; Roll-Hansen, 1972). Kohh (1964) found attacks by *Gremmeniella abietina* in 30 to 50-year-old stands of Scots pine, of German provenances, in the south of Sweden to be correlated with frost damage during the winter of 1952/53 and with the unusually dry summers in 1955 and 1959. The devastating effects caused by *Gremmeniella abietina* on imported pines in Sweden were pointed out by Björkman (1961). However, attention had already been drawn to this problem by the Norwegian pathologist Brunchorst as early as 1888. He observed that introduced pine species (*Pinus nigra, P. mugo*) were attacked by *Gremmeniella*, but not the native Scots pine. Heavy attacks by *Gremmeniella* were also reported by Kujala (1950) in young stands of lodgepole pine in Finland. He found that unthinned stands on productive sites, with high air humidity and poor ventilation, were predisposed to infection. Kujala found no difference in the degree of resistance of different tree provenances. He considered that this pathogen posed a very severe threat to the establishment of successful lodgepole pine plantations in Finland. However, Weissenberg (1975), who later investigated the stands previously examined by Kujala and Heikinheimo (1956) came to the conclusion that, with one exception, they had all recovered.

Donaubauer (1972), who gave an account of the distribution of *Gremmeniella abietina* in Europe and North America, found that most tree species which were planted far outside their natural geographical ranges, in cool and humid climates, were highly susceptible to attack. The needles of northern pine provenances have a high dry matter content during autumn and winter (Langlet, 1936). Experimental studies indicate a positive correlation between high dry weight of the needles and resistance to *Gremmeniella* (Teich, 1968; Dietrichson, 1968). Dietrichson also found a relationship between increasing northern latitude of provenance, degree of needle and shoot extension, and resistance to *Gremmeniella*.

Extremely heavy attacks by *Gremmeniella* in eastern Norway were recorded by Roll-Hansen (1964, 1967, 1969, 1972) and Roll-Hansen & Roll-Hansen (1973). "Fysiogenic diseases, for example caused by heavy snow cover, extremely cold summers with much frost, or strong direct or indirect insolation above the snow cover in the last part of the winter, were also undoubtedly of great importance, directly and indirectly, by furthering attacks by the fungus" (Roll-Hansen, 1972). However, Reid (1967) could find no relationship between frost action and attacks by *Gremmeniella* (*Brunchorstia*) in Great Britain. On the other hand, Pomerleau (1971) found extensive damage by *Gremmeniella* on conifers in Quebec, Canada, related to summer frosts during the most critical growth period. Dorworth (1972) also associated this pathogen with frost damage primarily in topographical depressions i.e. frost pockets. Hiratsuka & Funk (1976) reported *Gremmeniella* on exposed small trees of lodgepole pine in frost pockets in Jasper National Park, Alberta.

Donaubauer (1974) considered that the prior occurrence of frost damage was unnecessary for infection. Increased air humidity during the growth period or lack of sufficient light leading to retarded maturation of the host tissue, were conditions which predisposed to infection. Spore discharge depends on a sufficiently high relative air humidity (Smerlis, 1968; Skilling, 1969) which is higher after rain in dense stands, close to ground-level where evaporation occurs for a longer period of time. These observations explain the results reported by Kujala (1950) viz. that dense stands on productive sites with high air humidity and poor ventilation were predisposed to infection.

The pathogenicity of *Gremmeniella* or of its imperfect stage, *Brunchorstia*, has been investigated by several plant pathologists (Ettlinger, 1945; Bowen, 1940; v. Vloten & Gremmen, 1953). Most of their experiments yielded no definite proof of its pathogenicity. However, the severe attacks by *Gremmeniella* in nurseries in Sweden described by Björkman (1959) and the results of the inoculation experiments by Roll-Hansen (1964), Martinsson (1975), Kurkela & Norokorpi (1979), Hamnede (1980), Barklund & Rowe (1981), left no reason for doubt that this fungus was a primary pathogen. The reason for the failure of some of the inoculation experiments has been given by Reid (1968), who pointed out that *Brunchorstia* more commonly occurs on suppressed branches in healthy plantations, thus favouring a natural pruning of the trees and "that the normal role of the fungus is not that of a virulent parasite" and that "*Brunchorstia* normally plays an important role in the maintenance of a natural system of forest hygiene". This role has also been pointed out by Kohh (1964).

Gremmeniella abietina is considered to be indigenous to Europe because of the existence of some relatively resistant phenotypes of *Pinus* spp. (Dorworth, 1974). This pathogen has been known in Europe since the end of the nineteenth century, but its attacks have often been ascribed to other fungi. It was recorded later in North America, on several pine species. The first find was made in the 1930s on *Pinus resinosa* Ait. in Ontario, but the pathogen was not identified until 1964, when apothecia of *Gremmeniella* were observed on cankered twigs of *Pinus resinosa* (Ohman, 1966). Many epidemics in the 1960's have been ascribed to *Gremmeniella* (Schneider, 1961; Martin, 1964; Punter, 1967).

The first discovery of this pathogen on lodgepole pine in Canada (Quebec) was made by Smerlis (1968). Not until the mid 1970's it was found on lodgepole pine growing within its natural distribution area in western Canada, but lodgepole pine introduced into the Canadian provinces of Ontario and Quebec has proved to be extremely susceptible (Dorworth, 1974). Contrary to Dorworth (1975), Hiratsuka & Funk (1976) considered that *Gremmeniella* formed part of the indigenous flora and did not represent a recent westward spread of the fungus from eastern North America. There are reasons for believing that *Gremmeniella* was described under the name of *Cenangium ferruginosum* as early as in the 1920's (cf. Weir, 1921; Laidlaw, 1983). This is probably why no severe epidemics of *Gremmeniella* have been reported in western North America. A more virulent strain of *Gremmeniella abietina* was reported in eastern North America in the 1970's (Skilling, 1977), causing severe damage to red pine, *Pinus resinosa*.

Stem damage as a predisposing factor to infection by pathogens

Vole damage. Hitherto vole damage has posed the most severe threat to *Pinus contorta* in northern Sweden. Experiences have been similar in Norway (Roll-Hansen & Roll-Hansen, 1977) and in Finland (Annila et al., 1983). Two of ten trials in the study series (Hornmyr and Pausele) suffered severe damage during the investigation period. The severity of vole damage to *Pinus contorta* is alarming. Even though lodgepole pine is capable of surviving repeated attacks by voles, growth is hindered and wood quality suffers, and the injuries to the bark often provide ingress for secondary pathogens. Infection by *Gremmeniella abietina* was recorded two to three years after the vole peak during the winter of 1977/78 (Hornmyr, Fig. 22). Also northern provenances of lodgepole pine were infected. During 1984, infection by *Gremmeniella* was more severe. As a consequence of a higher inoculum level, even trees that had not been attacked by voles were infected by *Gremmeniella*. Preliminary results from provenance trials with lodgepole pine in the far north of Sweden (Nattavaara, Tärendö) indicate a similar development (Karlman, unpublished).

It is possible that a provenance trial is a more favourable environment for the spread of pathogens than a conventional regeneration. Susceptible provenances are mixed with more resistant ones. The weather conditions were, however, very special during 1984 with great variations in temperature during May and June—summer temperatures followed by temperatures below 0°C. In addition July, August and September were months with high precipitation and thus favourable for the spread of pathogens.

Vole damage as a predisposing factor to infection by pathogens will be discussed in a subsequent paper.

Pruning. Some findings of *Phacidiopycnis pseudotsugae* in the provenance trials are of special interest because this fungus was also recorded by the author on dying *Pinus contorta* trees in a pilot study made in western Dalarna and northern Värmland (in central Sweden) of the effects of pruning *Pinus contorta*. Interest in pruning of Scots pine and lodgepole pine has increased in Swedish forestry in recent years. By pruning it is possible to raise the quality of wood considerably. Scots pine has been pruned for many years without any discernible problems, for the trees were mainly pruned during the growing season. The need for creating year-round employment has, however, caused pruning during winter dormancy to become economically interesting.

In the pilot study, more than one third of the trees pruned in September and October 1981 and 1982 were killed during the following autumn (Karlman, 1985). Trees pruned during spring and summer were completely unaffected. *Pinus contorta* has a thin bark, and the risks of fungal infection in autumn are enhanced by pruning because the tree is unable to mobilize its defence mechanisms, i.e. compartmentalization and callus formation. In addition, the frequency of fungal spores in the air is higher in autumn than in summer.

Other fungi

Sclerophoma pityophila frequently occurs in the provenance trials associated with various types of primary damage caused by voles, elk, insects, unfavourable weather conditions, and parasitic fungi. *Sclerophoma* is occasionally a secondary pathogen, but is usually a completely harmless saprophyte. Inoculation experiments made by Smerlis (1970) have, however, demonstrated the role of *Sclerophoma pityophila* as a pathogen. In the provenance trial at Moskosel, *Sclerophoma* was mainly recorded on weather-damaged plants and following infection by *Gremmeniella abietina*. In the literature dealing with forest pathology, *Sclerophoma pityophila* has frequently been reported as causing severe damage to Scots pine (Wilson, 1925; Nazarova, 1936; Kujala, 1950), the symptoms being similar to those produced by Melampsora rust (*Melampsora pinitorqua*). There are reasons for suspecting that two or three month-old attacks by *Melampsora* have sometimes been erroneously attributed to *Sclerophoma*; *Melampsora*-infected shoots are often invaded by pycnidia of *Sclerophoma* later in the autumn. By this time it can be difficult to discern the scars caused by *Melampsora* during summer. According to Roll-Hansen (1967), *Sclerophoma* is found only as a saprophyte in Norway.

Lachnellula flavovirens, a species closely related to the northern pine canker, *Lachnellula pini* (Fig. K), is often associated with infection by snow blight, *Phacidium infestans*. According to Björkman (1948) the northern pine canker (*Dasyscypha fuscosanguinea*) frequently occurs on the branches and needles of Scots pine following snow blight infection. *Lachnellula pini*, which is the correct name for the northern pine canker, has previously been confused with the saprophytic *Lachnellula* (*Dasyscypha*) *fuscosanguinea*, a closely related species which occurs on *Pinus cembra* in the Alps. These two fungi have completely different hymenia: *L. pini*—orange-coloured, *L. fuscosanguinea*—pink-coloured. The apothecia and spores of the *Lachnellula*-species which were found on the dead needles and branches of *Pinus contorta* attacked by snow blight are somewhat smaller than those of *Lachnellula pini*. Kurkela & Norokorpi (1979) have shown that in most cases the latter is a true saprophyte and is identical with *L. flavovirens*. Thus this species must not be confused with the closely-related *L. pini*, which is a severe pathogen on Scots pine on very dry sites such as the lichen-rich pine forests in Norrland.

Minor attacks by the honey fungus, *Armillaria* sp. and *Heterobasidion annosum* (*Fomes annosus*), have been mainly recorded on the lodgepole pine trials planted in 1967 (Ånge, Edsele, Volgsele). These pathogens may increase in importance in the future (Laine, 1976). However, *Armillaria* sp. frequently occurs in regenerations of lodgepole pine in western Canada without being a serious problem.

Figs. G–H. The source of infection in 1978 and the result three years later in the provenance trial at Moskosel.

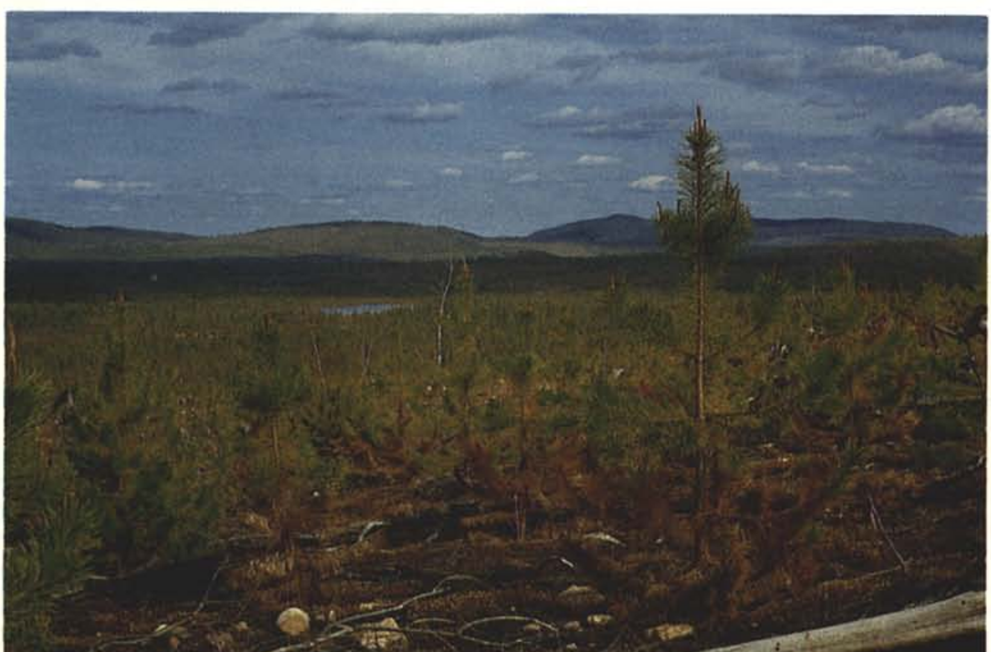


Fig. J. Infection by *Gremmeniella abietina* on lodgepole pine. Note the brown bases of needles.

Fig. K. Apothecia of the northern pine canker, *Lachnellula pini*, on stem of lodgepole pine at Moskosel.

In summary, damage by parasitic fungi to young plants and trees of *Pinus contorta* in northern Sweden has up to 1984 been relatively unimportant in the case of the more northern provenances, with the exception of *Gremmeniella* infection after vole damage and *Phacidium infestans* attack in high-altitude stands. In a nursery, northern provenances of *Pinus contorta* have been severely infected by *Sirococcus strobilinus* (Karlman, 1980), a parasitic fungus recorded on *Picea abies* in Sweden and commonly found on lodgepole pine in nurseries in western Canada (Illingworth, 1973). In the central parts of northern Sweden most provenances of *Pinus contorta* grow excellently (Ånge, Edsele), and northern provenances are remarkably productive on the northernmost site despite a high frequency of *Phacidium infestans* (Moskosel). Later investigations indicate, however, more severe damage to *Pinus contorta* with increasing latitude and altitude in northern Sweden. Especially the severity of *Gremmeniella* infection after vole damage during 1984 is alarming (Karlman, unpublished).

As regards the risk for a calamity in connection with introduced pathogens, the greatest risk is not that *Pinus contorta* may become infected by an alien fungal species, but that the infection might spread to the native conifer *Pinus sylvestris*. This is the real problem. If a pathogen attacking lodgepole pine increased to epidemic proportions in extensive stands of *Pinus contorta*, it could very easily spread further and infect Scots pine. The bigger the source of infection, the less is the resistance of the plants (van der Plank, 1975). In addition it is known that some of the rust fungi found on *Pinus contorta* in western Canada can infect *Pinus sylvestris* as well, e.g. *Endocronartium harknessii* and *Cronartium comptoniae* (Ziller, 1974). Thus it must be of the utmost importance to prevent any introduction into Scandinavia of pathogens from western Canada or other countries (cf. Karlman, 1983).

Mortality related to weather damage and infection by pathogens

The overall survival rate of the trees at Moskosel nine years after planting is remarkably high—despite the northern latitude of the site (Fig. 28). According to Rosvall & Strömberg (1980), the southern provenances of lodgepole pine had already suffered from weather damage in the nursery, probably due to poor winter acclimatization. This damage was first noticeable after shoot elongation occurred in the following spring, by which time the majority of the plots of the Institute's series of trials had already been planted up. Because of this, some losses were recorded even in the first year after planting, e.g. in the provenance trial at Hornmyr (Fig. 30). In the Moskosel trial, which was the last trial of the series to be planted, shoot elongation occurred at planting time and any damaged seedlings could immediately be sorted out and rejected. The results of subsequent investigations (Karlman, unpublished) indicate that the northern provenances can also suffer from severe damage when inadequately acclimatized previously in the greenhouse.

Vole damage and severe weather damage occurred four to five years after planting, and such plants became infected by parasitic fungi one to three years after this primary damage had occurred. In one trial of ten, high mortality rates were recorded among provenances of lodgepole pine after repeated attacks by voles (Pausele), and after repeated browsing by elk and deer (Alnö). Northern provenances of *Pinus contorta* suffered from infection by *Phacidium infestans* four years after planting (Moskosel)—Scots pine two to three years later—but this only resulted in a small loss of increment, and a relatively small number of plants actually died. Snow blight infection, however, caused heavy losses to Scots pine six to seven years after planting at Hornmyr (Karlman, 1984).

Concluding remarks

This nine-year study of pathogens on *Pinus contorta* in northern Sweden indicates that:

- Damage to *Pinus contorta* primarily occurs during the first ten years after planting. Only minor damage has been recorded in the provenance trials from 1967 during the investigation period.
- Northern provenances of *Pinus contorta* are generally more resistant to pathogens than southern provenances.
- The most important cause of mortality among southern provenances of *Pinus contorta* has been weather injuries due to poor winter acclimatization in the nursery, which led to high mortality rates already during the first year after planting.

● Weather damage occurs almost every year among trees of southern provenance.

● Trees from coastal provenances were severely damaged by frost during unfavourable weather conditions, i.e. the extremely cold winter of 1978/79 in northern Sweden.

● Even trees of northern provenance of lodgepole pine have suffered from weather damage due to temperature oscillations during shoot elongation. However, only minor damage has been recorded.

● Severe weather damage is a predisposing factor to infection by secondary pathogens, primarily *Gremmeniella abietina*. There is a minor correlation between severe weather damage and *Phacidium infestans*.

● There is a clear tendency for a diminution in the severity of attacks by both *Gremmeniella* and *Phacidium* with increasing latitude and altitude of provenance in the more southern sites (i.e. Stensvattnet).

● Even northern provenances of *Pinus contorta* are infected by *Phacidium infestans* in high-altitude stands in northern Sweden. However, snow blight infection is of less importance to lodgepole pine than to Scots pine due to the rapid early growth of the former.

● The more bushy branches of *Pinus contorta* more readily intercept fungal spores of *Phacidium infestans* than do those of Scots pine of equal age, when exposed to the same source of infection.

● Seedlings of Scots pine were infected 1–3 years after those of lodgepole pine.

● The most productive plants of both *Pinus contorta* and *Pinus sylvestris* are attacked by *Phacidium infestans*. Plants not infected by snow blight have a lower mean height than those infected. Not until 50% of the needles of the plant were infected (grade 3) was the height of the tree below average.

● Severe infection by *Gremmeniella abietina* has been recorded after vole attack even among northern provenances of lodgepole pine.

● The root rot fungus, *Heterobasidion annosum* and the honey fungus, *Armillari sp.*, occur more frequently in 12 to 15 year-old stands than in younger stands. No pronounced difference between provenances were found.

● *Pinus contorta* is practically resistant to *Melampsora* rust (*Melampsora pinitorqua*) and *Lophodermella* needle cast (*Lophodermella sulcigena*).

● Pinus sylvestris can be infected by *Lophodermella sulcigena* five years after planting.

● So far *Pinus contorta* has mainly been attacked by the same fungi as *Pinus sylvestris*, with the exception of *Melampsora* rust and *Lophodermella* needle cast. However, lodgepole pine is more susceptible to infection by *Gremmeniella abietina* in connection with vole damage, depending on the more severe injuries on lodgepole pine than on Scots pine.

● So far vole damage has been the most serious threat to *Pinus contorta* in northern Sweden.

● With respect to vole damage, the Tantalus Butte (62°08′) provenance was the most promising. The most severely *Gremmeniella*-infected provenance was that of Whitehorse (60°52′).

● Voles attack *Pinus contorta* even 14 years after planting.

● A great variation in survival rates has been found among experimental sites depending on the geographical location, climate, unfavourable weather conditions, frequencies of predators, etc.

● The most promising provenances at the northernmost site, Moskosel, are in rank (1 = best value):

	Height growth	Survival
Toad River (58°52′)	1	2
Whitehorse (60°52′)	2	5
West Summit Lake (63°03′)	3	4
Rusty Creek (63°30′)	4	1
Watson Lake (60°03′)	5	3

All show high values for mean height and survival rates, ranging between 93–98%. However, the frequency of *Phacidium infestans* is comparatively high, i.e. 26% within the Toad River (58°52′) provenance. The Scots pine provenance BD 428 (66°30′) has as good values with respect to mean height and survival as the Fort Nelson (58°50′) and the Tantalus Butte (62°08′) provenances. With respect to snow blight infection, the Fort Nelson (58°50′) provenance is very promising.

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