Resistance to Snow Blight (*Phacidium infestans* Karst.) in Different Provenances of *Pinus silvestris* L.

Resistens mot snöskytte hos olika tallprovenienser

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In 1923, GUNNAR SCHOTTE published a paper on "The provenance of the pine seed—the most important reforestation problem of northern Sweden". In this work the importance of using seed that is suitable for the site of reforestation was confirmed. It was also shown that it is particularly important not to move seed from a warm climate to a colder one. A change from a cold zone to a warmer one will, on the other hand, lead to good results.

So far as conditions in northern Sweden are concerned, it was shown that snow blight, caused by *Phacidium infestans* Karst. in many cases causes pine seedlings to die; but, as no annual observations had been made, the degree in which this disease is responsible for the differences which appear in various provenances could not be determined with certainty.

SCHOTTE was convinced, however, that snow blight in general, and more particularly in Upper Norrland, is more prone to attack seedlings from a milder climate than those deriving from a climate more similar to that of the cultivation area. He also claimed that seedlings from a harder climate seem to be even more resistant to snow blight than seedlings raised from seed from the locality.

Because no regular annual observations of the reasons of the seedling deaths had been undertaken, or experiments made with a uniform infection of comparable seedling material of different provenances, a further investigation of this problem, which is also of a great practical significance, was necessary. In all northern Europe, as well as in the higher elevations of the Alps, snow blight is namely an extremely serious obstacle to the reforestation of pine. Even though some seedlings survive, a strong deformation of the plants is regularly occurring, and the plantations are split by locally very severe attacks by the fungus. This is especially the case where the snow lies deep or where spreading of the fungus is promoted by other factors, such as dense sowing (cf. BJÖRKMAN, 1948). Since Schotte's observations suggest the likelihood of different provenances of pine being susceptible to attacks by this fungus in a very varying degree, it should be possible to find a practical way of controlling the disease genetically by selection and improvement of the resistance.

Consequently snow blight has long been of interest to scientists concerned with forest genetics (cf. LANGLET, 1934). Recommendations

as to the suitable limits for moving pine seed with regard to altitude and latitude have also been made because of *inter alia* the danger of attack by snow blight (LANGLET, 1945, 1957).

By pursuing in nurseries a programme of systematically planned experiments with different provenances of pine which had been inoculated at certain stages with mycelium from the snow blight fungus (BJÖRKMAN, 1948, pp. 83–85), it was for the first time possible to show experimentally that provenances from the inland of the northern parts of the country were less susceptible to attacks than other provenances. The "Ausbreitungsresistenz" (GÄUMANN, 1951), of which this is evidently an example, manifested itself in such a way that the mycelium from the infection point spread much quicker and could thus destroy a considerably larger quantity of needles on plants of southern origin than on plants of northern origin. Under similar experimental conditions, the attack diameter of pine seedlings from Enare träsk (68° 55' Lat. N) had for instance a mean value of only 90 mm after two years, whereas the corresponding values for pine seedlings from Vindeln (64° 11' Lat. N) were 168 mm and from Södermanland (59° 20' Lat. N) 228 mm. Similar results were also obtained from other experiments where the "infected needle volume" had been measured.

When the Swedish Forest Research Institute planned to conduct a very extensive provenance experiment with pine all over Sweden during the period 1951 to 1954, provision was also made for a number of special sample plots with a smaller amount of provenances from various parts of northern Sweden in order to investigate their possible resistance to snow blight. These sample plots were laid out at four different places in 1953, i.e.:

Rahaberget, Kåbdalis, in the province of Norrbotten, 66° 19′ Lat. N, 440 m above sea-level

Svartberget, Vindeln, in the province of Västerbotten, 64° 14' Lat. N, 200 m above sea-level

Himmeråsen, Idre, in the province of Dalecarlia, 61° 54' Lat. N, 756 m above sea-level

Högståsen, Orsa, in the province of Dalecarlia, 61° 05′ Lat. N, 365 m above sea-level.

The planting of these sample plots was for the most part handled by Mr. VILHELMS EICHE, to whom I wish to extend my warm thanks for his valuable help and co-operation.

Experiment schedule

In 1950 and 1951, pine cones were collected by Mr. EICHE from a great number of places in Sweden and Norway situated at different latitudes and also to a certain extent at different altitudes. The northern provenances (Nos. 1 to 38) were sown in a nursery at Sundmo (63° 34' Lat. N) in the spring of 1951, while seeds from Lat. 62° and southwards were sown in a nursery at Bogesund outside Stockholm (59° 23' Lat. N) in the same year. Two years later the seedlings were transplanted and put out during the spring of 1954 as 2 + 1 plants on a number of prepared sample plots all over the country.

From the plants thus raised 20 different provenances were selected, representing different northerly latitudes as well as inland and coastal districts. From the inland areas plants were raised from seed collected from both high and low altitudes. The coastal provenances included seed from the Arctic, Atlantic and Baltic coasts. These provenances were planted on the four sample plots for infection experiments with the snow blight fungus. Plants of the same provenances, but deriving from seeds collected from individual trees within the population, were also put out on the sample plots.

At each experimental site, the seedlings were planted in the spring of 1954 with four plots of each provenance, i.e. a total of 80 plots. The size of the entire experimental area at each site was thus 20×19.2 m and the size of each plot 2.0×2.4 m. In [each experimental area, 3,200 plants were put out with 40 seedlings per plot spaced at 40×30 cm. There were thus $4 \times 40 = 160$ plants of each provenance in each area. At Idre, the plants were put out more sparsely, the spacing of plants there being twice that of the other plots. This experimental area was consequently larger than the others.

On the whole, the plants developed very well in 1954 and 1955, but certain repair planting had to be carried out, particularly in the plantation at Idre. For this purpose, plants earthed near the station and of the same provenance were used. In the plot with plants from Bavaria in Germany practically all the plants died during the first year because of their low resistance to frost. In the experimental area at Kåbdalis in the very north most of the plants, which had been raised at Bogesund, died at an early stage. It is probable that insufficient precautions had been taken to prevent the drying of the plants used on the snow blight plot, either during transport or in connection with planting. All plants raised at Sundmo developed well.

In the third autumn after planting (1956), when the plants had become acclimatized and had made leading shoots normal for the provenance (cf. the figures of plant height in Table 1), they were inoculated with small branches of pine infected by snow blight during the previous autumn and winter. The needles of these branches, which were about 7 to 8 cm long, were all infected with snow blight, which at this time had opened its apothecia and started delivering mature spores (cf. BJÖRKMAN, 1948, 1961 b). When making the inoculation, great care was taken to avoid uncontrolled distribution of the spores. For this reason the infected material was kept in separate plastic bags for each infection point. Four different points were distributed equally within each plot. Inoculation was in all cases made at the last whorl of branches on the plants; but in the case of plants that were so big that this point would be too high above the snow cover and too high with regard to their uniformity with plants of other provenances, the inoculation was made at the second whorl of branches counted from the top. In all cases the point of infection was therefore situated about 1 to 1.5 dm above the ground; this has been found to be a favourable position for the development of the fungus. All other plants were sprayed with lime-sulphur. During the first winter, the fungus developed about 5 to 10 cm from the infection points, chiefly because of the spreading of mycelium over the needles of the infected plants.

No new inoculation and no spraying were made in the autumn of 1957. The intention was that the snow blight infection should spread from the points already contaminated. This also occurred very uniformly in the following winters, so that by the winter of 1958/59 practically all the plants had been reached by the mycelium of the snow blight fungus growing in the snow. It was therefore possible to register the susceptibility of the plants with great accuracy. In some cases, a spore infection had also taken place in the winters of 1957/58 and 1958/ 59, so that a new "unexpected" infection had occurred. This would in some degree affect the regularity of the experiment, but its influence on the infection picture obtained at the examination in the summer of 1959 was insignificant. The fungus had then spread very evenly over all the infected plots as far as the plants were susceptible to heavy attacks. Thus, the values of "volume dead needles" may be considered as the best way of determining the resistance of different provenances (Table 1).

The registration made in the summer of 1960 showed that the most sensitive plants had died and that living plants were often deformed with dead annual shoots, but with big secondary shoots. A correct

result would therefore not be obtainable by measuring the height of the plant, nor would the "volume dead needles" any longer have given an adequate expression of the resistance, as most of the needles attacked during the winter 1957/58 had been shed. An exception from this general development cycle was found in the experimental area at Idre where, following the infection in October 1956 to obtain natural infection points, accidental spraving of all plants with lime-sulphur occurred. The result was that only limited infections occurred in the winter of 1957/58, which explains the low numbers of dead and dying plants that winter (Table 1). In general, however, this retardation was overcome during the following winter. It has therefore been possible to use the 1959 inventory of "volume dead needles" as the best expression of resistance to snow blight even in the case of the Idre experimental area. The figures for this area, however, are lower than at the other sites; a contributory factor in this respect might be the greater spacing of plants used in the plots at Idre, thereby making it more difficult for the snow blight fungus to attack the surrounding plants. Consequently the experiment at Idre should not be regarded as being quite comparable to the other experiments, but rather as a complement to them. Because as already mentioned half of the plants in the Kåbdalis experiment died in the first year from other causes than attack by snow blight, our conclusions regarding the resistance of different pine provenances to snow blight are founded chiefly on the registrations made in the plots at Orsa and Vindeln.

A final inventory of all the experiments was made in the summer of 1960, when the number of dead or dying plants in each plot was registered.

In several cases the complementary experiments with rows of plants raised from seed from individual trees within the same pine population, which were laid out in a large number of plots, showed a clear tendency to greater resistance in the progeny of certain trees than in that of others. However, due to the irregularity of the spreading front of snow blight mycelia under the snow cover, and to the fact that only a small number of plants was available for the experiments, no final conclusions can be drawn in this respect.

Results of the experiments

Table 1 shows that already after one winter's infection, there was a general increase in the number of dead or dying plants in all the sample plots the more southerly the provenance place of the seed. The provenances from northernmost Norway, however, showed a somewhat greater mortality than the more southerly provenances from the inner parts of Upper Norrland. This circumstance became still more evident the following year (Table 1).

In 1959, the number of dead and dying plants was greatest in the experimental area at Kåbdalis. With the exception of a few samples



Figure 1. Dead and dying plants of 7 year-old *Pinus silvestris* L. of different provenances inoculated with *Phacidium infestans* Karst. Observations in July 1959 at four different experimental plots of each provenance after 2 years' attack.

from the inland of Upper Norrland, plant mortality was here 100 % later on (1961). The greatest number of dead plants was recorded for the southern provenances on the sample plots at Orsa, while provenances from the interior of Norrland were found to survive more uniformly (Figure 1).

Tab. 1. Development of *Pinus silvestris* plants of different seed sources and extent of attack by *Phacidium infestans* after 1 and 2 years respectively. *Phacidium* inoculated in October 1956 at 10 cm height on 4-year plants planted in 1954 on four experimental plots at KÅBDALIS ("K", Lat. 66° 16', Long. 19° 53', elevation 440 m above sea-level), VINDELN ("V", Lat. 64° 14', Long. 19° 43', elevation 200 m), IDRE ("I", Lat. 61° 54', Long. 12° 46', elevation 756 m), ORSA ("0", Lat. 61° 05', Long. 14° 58', elevation 365 m) in North Sweden. The fungus developed in the winters 1957/1958 and 1958/1959 over all plants. Figures from Oct. 1958 and Oct. 1959 (italics).

Seed sources (provenance)	Lat. N	Long. E	Eleva- tion above sea- level m	Dry sub- stance per cent accord- ing to LANG- LET	Plant height Oct. 1956 average cm				Dead and dying plants per cent 1958 and <i>1959</i>				Volume dead needles, per cent of total needle volume 1958 and 1959			
					к	v	I	0	К	v	Iı	0	к	v	I1	0
Moen	69° 07′	18° 35′	100	40.87	23	26	18	27	$16.0 \\ 50.0$	9.5 26.5	$\begin{array}{c} 3.0 \\ 21.5 \end{array}$	$7.0 \\ 24.5$	54.0 73.6	55.6 57.8	$14.1 \\ 42.3$	54.7
Tranöy	$68^{\circ} 1\overline{1'}$	15° 35′	10	39.41	20	25	14	25	$\begin{vmatrix} 24.4 \\ 42.5 \end{vmatrix}$	$\frac{10.5}{48.0}$	$\begin{array}{c} 4.5\\ 15.5\end{array}$	11.5 17.0	$\begin{array}{c} 57.3 \\ 85.2 \end{array}$	51.6 59.3	$\begin{array}{c} 12.2 \\ 43.6 \end{array}$	$\begin{array}{c} 40.1 \\ 65.6 \end{array}$
Kitkiöjoki	$67^{\circ} 45'$	23° 22′	225	40.87	18	25	13	28	$\begin{array}{c} 16.0 \\ 32.5 \end{array}$	$\begin{array}{c} 8.5\\ 21.5\end{array}$	$\frac{1.0}{15.0}$	14.0 16.0	$38.2 \\ 60.5$	$\begin{array}{c} 29.3\\ 35.4 \end{array}$	$\begin{array}{c} 6.9 \\ 25.8 \end{array}$	$\frac{33.6}{36.5}$
Korpilombolo	66° 53′	23° 03′	175	40.21	22	27	19	28	$10.0 \\ 29.5$	$\begin{array}{c} 12.5\\ 19.0 \end{array}$	$\begin{array}{c} 3.5\\ 15.5\end{array}$	$\frac{11.5}{16.5}$	$\begin{array}{c} 36.0 \\ 54.8 \end{array}$	25.6 29.4	$5.4 \\ 24.6$	$\begin{array}{c} 27.7 \\ 32.2 \end{array}$
Moskosel	$65^{\circ} 5\overline{4'}$	19° 15′	360	40.06	22	26	18	28	$\begin{array}{c} 8.0\\ 32.0\end{array}$	$\frac{12.0}{16.0}$	$5.0\\16.5$	$\begin{array}{c} 12.0\\ 15.5 \end{array}$	46.4 62.3	34.6 35.6	$\begin{array}{c} 7.0 \\ 28.7 \end{array}$	$\begin{array}{c} 30.2\\ 36.9 \end{array}$
Vilhelmina	64° 35′	16° 50′	350	39.42	26	32	19	31	54.0 43.0	$21.5\ 35. heta$	8.0 16.0	$\begin{array}{c} 15.5\\ 19.0 \end{array}$	$\frac{51.9}{62.2}$	$\begin{array}{c} 41.5\\ 46.0 \end{array}$	$\begin{array}{c} 13.4\\ 44.6\end{array}$	$\begin{array}{c} 37.8\\ 49.9 \end{array}$
Robertsfors	$64^\circ 12'$	20° 48′	50	38.91	28	30	23	34	$\begin{array}{c} 47.0 \\ 56.5 \end{array}$	$\begin{array}{c} 29.5\\ 34.5\end{array}$	5.5 27.5	$\begin{array}{c} 20.0\\ 22.0 \end{array}$	$\begin{array}{c} 73.3\\ 81.3 \end{array}$	52.5 57.0	$\begin{array}{c} 15.7 \\ 60.1 \end{array}$	49.0 69.2
Örträsk	$64^{\circ} 08'$	18° 39′	475	39.31	26	30	19	36	$\begin{array}{c} 28.0 \\ 46.0 \end{array}$	$\frac{18.0}{29.0}$	$5.0 \\ 21.5$	$\begin{array}{c} 16.0 \\ 20.0 \end{array}$	$\begin{array}{c} 63.2\\ 69.4 \end{array}$	$\begin{array}{c} 46.3 \\ 60.4 \end{array}$	$\frac{10.9}{55.0}$	$\begin{array}{c} 43.8 \\ 65.0 \end{array}$
Vallbo	63° 10′	$13^{\circ} 04'$	540	39.16	24	29	18	36	$\begin{array}{c} 47.5 \\ 65.0 \end{array}$	$\begin{array}{c} 23.5 \\ 44.0 \end{array}$	$\begin{array}{c} 14.0 \\ 41.0 \end{array}$	$\begin{array}{c} 20.0 \\ 27.5 \end{array}$	75.7 77.0	55.7 57.4	$\frac{15.2}{51.2}$	$52.9 \\ 63.1$
Brämön	$62^\circ12'$	$17^{\circ}42'$	5	37.98	-	26	24	58	100	$\begin{array}{c} 31.3\\ 62.0 \end{array}$	$\begin{array}{c} 26.0 \\ 34.0 \end{array}$	$\begin{array}{c} 20.0\\ 25.5\end{array}$	-	$72.3 \\ 74.3$	17.6 66.4	$\frac{65.7}{76.7}$
Sveg	$62^{\circ} 03'$	14° 19′	385	38.33		37	25	42	100	$\begin{array}{c} 27.0\\ 32.0 \end{array}$	$\begin{array}{c} 13.5\\ 25.5\end{array}$	$\begin{array}{c} 16.5 \\ 21.0 \end{array}$		$\begin{array}{c} 60.5 \\ 66.1 \end{array}$	$\frac{13.3}{56.2}$	$\begin{array}{c} 55.6 \\ 67.6 \end{array}$
Bunkris	6 1 ° 27′	13° 28′	550	38.26]	41	23	52	100	$\begin{array}{c} 21.0 \\ 46.0 \end{array}$	$\begin{array}{c} 7.5 \\ 22.5 \end{array}$	$18.5 \\ 32.5$	[$\begin{array}{c} 64.4 \\ 71.6 \end{array}$	$\begin{array}{c} 12.5 \\ 65.8 \end{array}$	$\frac{53.4}{66.4}$
Orsa	$61^{\circ} 05'$	14° 58′	365	37.70		40	$\left 22 \right $	44	100	$\begin{array}{c} 46.5 \\ 87.0 \end{array}$	$\begin{array}{c} 11.5 \\ 29.5 \end{array}$	$\begin{array}{c} 22.5\\ 24.5 \end{array}$		75.0 85.2	$\frac{16.7}{70.2}$	$rac{60.2}{75.8}$
Älvkarleby	$60^\circ 32'$	17° 33′	35	36.97	-	41	23	55	100	$\begin{array}{c} 86.5\\97.5\end{array}$	$\begin{array}{c} 20.0 \\ 71.0 \end{array}$	$\begin{array}{c} 26.5 \\ 29.5 \end{array}$		89.7 91.0	$\frac{20.0}{78.8}$	$\begin{array}{c} 70.3 \\ 84.0 \end{array}$
Bergen	$60^\circ 12'$	$05^{\circ} 23'$	50	36.49		41	22	61	100	99.5 100	$\frac{28.5}{74.5}$	$\begin{array}{c} 31.0\\ 45.5 \end{array}$	-	$\left. \begin{array}{c} 93.1 \\ 96.4 \end{array} \right $	27.5 <i>82.0</i>	$\frac{82.6}{88.7}$
Vinje	59° 35′	07° 50′	550	37.18	-	40	18	56	100	$\begin{array}{c} 62.5 \\ 67.0 \end{array}$	$\begin{array}{c} 10.5 \\ 66.0 \end{array}$	$\begin{array}{c} 26.0 \\ 57.5 \end{array}$		$69.6 \\ 78.3$	$\begin{array}{c} 13.6 \\ 72.4 \end{array}$	$\frac{59.1}{77.3}$
Eckersholm	57° 36′	14° 13′	225	36.25		39	23	60	100	$\begin{array}{c} 82.5\\ 100 \end{array}$	$\begin{array}{c} 29.5 \\ 82.5 \end{array}$	39.5 66.3	-	$\begin{array}{c} 93.5 \\ 100 \end{array}$	$\begin{array}{c} 29.2 \\ \$1.4 \end{array}$	$\begin{array}{c} 79.5\\ 96.4 \end{array}$
Kinnared	$57^{\circ} 01'$	13° 05′	140	35.74	-	43	27	61	100	$\frac{85.5}{100}$	$\begin{array}{c} 32.5\\ 82.5 \end{array}$	$\begin{array}{c} 37.0\\ 66.3 \end{array}$		$\frac{92.0}{100}$	$\begin{array}{c} 23.8\\ \$1.4 \end{array}$	$\frac{90.0}{96.4}$
Brömsebro	56° 18′	$16^{\circ} 02'$	15	35.25	-	41	28	58	100	99.5 100	$\begin{array}{c} 45.0 \\ 84.5 \end{array}$	48.0 71.0		$\begin{array}{c} 94.4 \\ 100 \end{array}$	29.0 86,5	$\frac{\overline{92.6}}{92.9}$

 1 Inhibited growth of the *Phacidium*-mycelium because of lime-sulphur treatment of plants in October 1956 before the inoculation (cf. the text).

If the snow blight attack was estimated as "volume dead needles" as a percentage of the total needle volume, very even values were obtained—especially after two years' attack (Table 1, Figure 2) which clearly confirmed the greater resistance of the northern provenances from the inland parts than that of provenances from coastal regions. Further, the very great susceptibility to attack of southern provenances (Plate I and II) was shown. On the whole the coastal provenances showed a greater susceptibility than the inland provenances from about the same latitude. Pine plants from Vinje in Norway



Figure 2. Volume dead needles on 7 year-old plants of *Pinus silvestris* L. of different provenances inoculated with *Phacidium infestans* Karst. Observations in July 1959 at four different experimental plots of each provenance after 2 years' attack.

situated 550 m above sea-level at 59° 39′ Lat. N generally showed a considerably greater resistance than did the plants from the coastal zones in the west and east at about the same latitude (from Bergen 60° 12′ and Älvkarleby 60° 32′, respectively).

The investigations, which on the whole confirm earlier findings and the results of previous small scale experiments, thus show that damage from snow blight may be limited by using provenances from places situated more to the north of the reforestation area, However, no completely invulnerable provenances have yet been found, even though some of the plants in plots planted with northern provenances did in fact escape infection altogether (cf. Plate II). In no case, however, did this concern plants that had been subjected to direct infection, but only those that had not been attacked by the mycelia spreading from the directly infected plants; the penetration of the mycelia in this case took place considerably slower than on plants of more southern provenances or which came from coastal regions (cf. Plate I). As can be seen from ENEROTH's investigations (1927) there is reason to believe that plants from lowland seeds raised in high-lying sites are more susceptible to snow blight than plants deriving from highland seed. Experiments concerning this question are at present being made.

Various provenances of the snow blight fungus have been tested in some smaller experiments at Svartberget, Vindeln. Thus, pine plants originating from the local area were inoculated with infected needles both from Upper Norrbotten and from the site, as well as from the interior of Ångermanland and finally from Idre in north-western Dalecarlia. No differences in the extent of the attacks could be observed however.

The so-called provenance question in northern Scandinavia is probably to a very great extent a snow blight problem. It has not been possible to determine, by investigating dead trees of various provenances in the old sample plots once used by SCHOTTE, for instance, in what degree this really is the case. The experiments described here can, however, be regarded as proof of the great significance of snow blight in this connection. The southern provenances have thus been completely eradicated by *Phacidium infestans*. It has as a rule been possible to follow the attack sequence in detail as shown in Table 1. This has not been possible in earlier experiments.

According to LANGLET, the dry substance content of the needles gives a value that characterizes the physiological condition of the plants during autumn and winter, i.e. the time of the year when the needles are attacked by snow blight. It has been found that the dry substance content may be calculated on the number of days when the average temperature was $+6^{\circ}$ C and above, also taking into consideration the degree of northerly latitude. The time during which the temperature exceeds $+6^{\circ}$ C—by LANGLET considered to be the vegetation period or at least proportional to it—may in turn be calculated on the degree of northerly latitude and the height above sea-level. The calculated value of the dry substance content (LANGLET, 1936, p. 357) will thus be founded on both the latitude and the height above sea-level as the corresponding average temperature conditions.

In Table 1 the extent of the snow blight attacks in the infection experiments has been put together with figures based on northerly latitudes and heights above sea-level. In the same table, the dry substance contents calculated by LANGLET on the investigated provenances, or in plants deriving from the locality (cf. LANGLET, 1936), are shown. From Table 1 it can be seen that higher dry substance content in the needles during winter corresponds rather regularly to less extensive attacks on the needles after snow blight inoculation. It is very likely not the dry substance content in itself that is of importance to the development, but some other factor which interacts with the dry substance content. Much speaks in favour of the influence of the osmotic pressure in the needle cells, which rises with increasing dry substance and sugar content, thus bringing about a decrease in the freezing-point adapted to the actual type of climate. In consideration of the attack intensity of the fungus in several other cases, one could, of course, expect that a higher sugar content in the cellular tissues of the host would be attractive to the fungus. On the other hand, it may be supposed that also the osmotic pressure in the fungus hyphae themselves must be greater than that in the cells of the host so as to facilitate the penetration of the fungus hyphae. Whether these physiological properties of the host and parasite are of decisive importance for the explanation of the resistance, which, no doubt, is to be found in northern provenances of Pinus silvestris, can, however, be determined first after special investigations of the cell content of the host and that of the parasite. An analysis of the difference between the cell content of pine and spruce needles would be helpful in investigations into these problems. It is known, namely, that spruce needles may be attacked by Phacidium infestans, but that this only happens with great difficulty and if the spruce needles are subject to a severe attack under particularly favourable conditions (BJÖRKMAN, 1948, Figure 64). It is further known that *Phacidium infestans* may attack other tree species too-e.g. Pinus cembra L. in the Alps (PETRAK, 1955)-but avoid others. A closely related fungus species will attack Abies species, especially Abies balsamea Mill., in north-eastern U.S.A. and Canada, but not Pinus species, etc. (REID & CAIN, 1962). A microchemical analysis of the cell content in various cases is of basic importance to resistance research.

Another physiological explanation of the resistance found in the northern provenances of *Pinus silvestris* may be a higher "cell activity" in connection with the respiration also at lower temperatures, compared to that in southern provenances transplanted to northern climatic conditions. Even entirely morphologic or anatomic differences, e. g. the cuticula of the needles, may in some cases be of significance in this respect. It is known for instance that the short, sturdy needles with thick cuticula that are to be found on suppressed pine plants, especially on pine heaths, show a remarkable resistance to attack by snow blight in comparison with thriving plants with large needles of the same provenance.

The real cause of the resistance is thus an extremely complicated question. It is probable that the various physiological or morphological properties of the host, which have been selected under a long period of development and adaptation to a certain type of climate, have some influence. It is naturally of the greatest interest that certain aspects of these basic causes of resistance should be investigated. On the other hand the conclusions that provenances exist that are more or less resistant to a certain parasite must be considered as a great step forward in the forest tree breeding work which is taking place, and of which the resistance to fungous diseases is a very important feature. In present forest tree breeding research into the Phacidium-problem, crossings between different pine provenances from different latitudes and altitudes are being tried. Preliminary observations concerning the field resistance of such plants have lately been made after infection with snow blight in October 1962. These experiments, which were made at Sundmo (63° 34' Lat. N) have hitherto, however, only been on a small scale. District differences in susceptibility to snow blight attacks have been found.

Present investigations are also being pursued along other lines; among other things regarding the possible differences in attacks by weak parasites on plants that for some reason have become weaker, e.g. by partial drying, snow pressure or very heavy thinning. In this connection special interest attaches to the attacks by Scleroderris lagerbergii (Lagerb.) Gremmen (Crumenula pinea (Karst.) Ferd. & Jörg., cf. BJÖRKMAN, 1959, 1961 a, 1963; HOLMGREN, 1961, 1963; EICHE, 1962; KOHH, 1963), which for the last five years or so have been prevalent in localities of pine in northern Sweden. Certain observations indicate that different pine provenances are unequally resistant to such attacks. Whether the varying dry substance content during the winter is directly or indirectly responsible for the degree of susceptibility also in these cases remains to be seen (cf. BIER, 1959). The extensive drying of plants that project above the snow cover during early spring seems, however, to be of primary importance, particularly in sites which are very exposed to winds (HOLMGREN, 1963), or in sites where direct sun radiation is particularly intense.

Summary

In conjunction with an extensive provenance experiment with pine conducted by The Department of Forest Genetics at the Swedish Forest Research Institute during the period 1951 to 1954, some special experimental plots were planted with 20 different Swedish and Norwegian provenances, so that eventual differences in their resistance to snow blight could be examined. Details of these areas, which were situated in Norrland and north Dalecarlia, can be seen in Table 1. The tested pine plants comprised vastly different provenances, from the coast of the Arctic Ocean down to southernmost Småland and Halland, and from different altitudes.

The experimental material was put out as 2 + 1 plants in the spring of 1954. In October 1956, four plants in each plot were inoculated with snow blight, and the remaining plants sprayed with a 3 % solution of lime-sulphur to protect them from attack. The inoculated plants were all attacked by the fungus, and during the following winter constituted natural seats of infection; details can be seen in Table 1 and Figs. 1 and 2. During the winters of 1957/58 and 1958/59 the snow blight infection spread from the infected points to affect the then unprotected plants in the various plots. Generally speaking the observations made earlier by Schotte (1923) and BJÖRKMAN (1948) were confirmed, i.e. that the resistance of the northern provenances is far greater than that of the southern provenances. On the other hand, plants which derive from seed collected from the coast of the Arctic Ocean showed a greater degree of susceptibility than did plants from the interior of Upper Norrland. With regard to the snow blight question, the removal southwards of plants of a more northerly origin than the cultivation area seems to be advisable, but not a removal from the south. Plants of northerly origin cultivated far to the south (north Dalecarlia) appear to be more resistant to snow blight than is the local provenance.

The physiological reasons for this resistance are considered; and it is feasible that the greater dry substance content in winter of needles on pine plants of northerly origin (LANGLET, 1936) is of indirect importance in this connection. Resistance tests on various crossings of different pine provenances are being made.

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Sammanfattning

Resistens mot snöskytte hos olika tallprovenienser

I anslutning till utläggning av ett stort proveniensförsök med tall genom avdelningen för skogsgenetik vid skogsforskningsinstitutet år 1951----1954 utlades även särskilda försöksytor med 20 olika svenska och norska provenienser i avsikt att pröva dessas eventuellt olika resistens mot snöskytteangrepp. Dessa försöksytor var belägna i Norrland och norra Dalarna såsom närmare framgår av tab. 1. De prövade tallplantorna representerade mycket olika provenienser från Ishavs-kusten ned till sydligaste Småland och Halland samt även olika höjdlägen.

Försöksplantorna utplanterades såsom 2/1 våren 1954. I oktober 1956 inokulerades 4 plantor inom varje parcell med snöskyttesvampen medan samtliga övriga plantor besprutades med 3 % svavelkalk och sålunda skyddades mot angrepp. De infekterade plantorna blev samtliga angripna av svampen och tjänstgjorde följande vinter som naturliga infektionshärdar såsom närmare framgår av tab. 1 samt fig. 1 och 2. Vintrarna 1957/58 och 1958/59 utväxte snöskyttesvampen från angreppspunkterna över de nu ej skyddsbesprutade plantorna inom de olika parcellerna. I stort sett har tidigare iakttagelser av SCHOTTE (1923) och Вjörкмам (1948) kunnat bekräftas, att nordliga provenienser är mycket mera resistenta än sydliga. Plantor som härstammar ur frö från Ishavs-kusten visade dock större mottaglighet än plantor från övre Norrlands inland. En förflyttning söderut av plantor av något nordligare ursprung än odlingsorten synes ur snöskyttesynpunkt vara att rekommendera men ej en förflyttning söderifrån. Plantor av nordligt ursprung odlade långt söderut (norra Dalarna) är av allt att döma mera resistenta mot snöskyttesvampen än ortens proveniens.

Den konstaterade resistensens fysiologiska orsaker diskuteras. Sannolikt har den under vintern högre torrsubstanshalten i barr av tallplantor av nordlig proveniens (LANGLET, 1936) en indirekt betydelse för plantornas resistens mot snöskytte. Försök pågår för närvarande med prövning av resistensen hos olika provenienskorsningar av tall.

- Plate I. An experimental plot of 7 year-old plants of *Pinus silvestris* L. from Orsa (61° 05' Lat. N) inoculated with *Phacidium infestans* Karst. Extensive attack by the fungus which after one winter spread very rapidly over the majority of plants (cf. Table 1 and Figure 2). Vindeln (64° 14' Lat. N) July 1958.
- Plate II. An experimental plot of 7 year-old plants of *Pinus silvestris* L. from Korpilombolo (66° 53' Lat. N) inoculated with *Phacidium infestans* Karst. Only relatively limited attack by the fungus after one winter (cf. Table 1 and Figure 2). Vindeln (64° 14' Lat. N) July 1958.





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