# FACTORS CAUSING MORTALITY OF TREE SEEDS AND SUCCULENT SEEDLINGS

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# Contents

	2-	-
1	ra	ge

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Introduction	3
Effect of temperature variation on dormant seed	5
Heat tolerance of seedlings	7
Drought tolerance of germinating seed	11
Drought tolerance of seedlings	12
Transpiration tolerance of seedlings	17
Cold (frost) tolerance	18
Seedings in field	20
Summary	25
References	27
Selostus	30

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# Introduction

A phase of the natural regeneration of forests takes place in an environment that is unique in many ways. Seeds and young seedlings of trees live in a limited space at the ground where the environment is extremely variable. However, little is known even about the factors which can be fatal to tree seed or seedlings. The factors vary with the seasons and weather, as well as with many biotic phenomena. In addition, the sites differ within short distances, for instance from a slash pile or grass tuft to a humus-covered patch or a minute crack where the mineral soil is denuded. The situation is further complicated by the sensitiveness of seed and succulent seedlings and by the fact that these must live at the ground where the microclimates vary greatly. For instance, the daily temperature amplitude may be 60° C in the thin surface layer of soil on certain forest sites but only 15° C on others (Vaartaja, 1954). To learn all the factors involved and determine their relative importance in forest regeneration requires comprehensive experiments under various conditions.

The reactions of trees to certain factors should be somewhat simpler to determine. However, not even the shade, heat, cold, and drought tolerance of the most important tree species in their early stages are known.

The investigations by Münch (1913), Baker (1929), Shirley (1936), Daubenmire (1943), and others have contributed considerably to our knowledge concerning the heat tolerance of seedlings. The problem was complicated by the phenomena of hardiness, self shading, and recovery, as well as by the effect of substratum and the size of seedlings. Altogether this problem has not yet been thoroughly studied.

Shade tolerance of a tree species is commonly confused with the concept of tolerance to overstory competition in general (Shirley, 1943). Determining shade tolerance in the way suggested by Shirley (1943) is more complicated than it appears because of the possible effect of fungi. Many common soil fungi may become pathogenic if the seedlings are shaded (Vaartaja, 1952).

Sporadic attention (Auer, 1948 and 1950; Barr, 1930; Borman, 1953; Daubenmire, 1943; Fabijanovsky, 1950; Karschon, 1949; Rohmeder, 1951; Shirley and Meuli, 1939; Smith, 1951) to the drought problem has shown that it is linked with various factors such as hardening, mineral nutrients, soils, transpiration conditions, development stage, and photoperiods. The knowledge of drought tolerance of any tree species, especially in their earliest stages, is far from complete. The same can be said of cold tolerance (S at o and M u t o, 1951).

Considerable loss in numbers of potential trees takes place when dormant seeds die or decrease in germination capacity. This may commonly happen, for instance, from attacks by fungi (V a a r t a j a, 1952), ants, or birds (V a a r t a j a, 1950) if germination is delayed. The optimum conditions for germination of tree seeds have been subjected to much study (see the review by B a l d w i n, 1942), but the complex and often adverse environment common in nature needs more attention. M o r k (1933, 1938, 1951) and A u e r (1950) have thrown some light on this problem by their studies on the germination of *Pinus silvestris* L., *Picea abies* (L.) Karst., *Larix europaea* Lam. et D.C., and *Betula* spp.

In the present study some simple but very little known environmental problems were explored, especially those which seemed most important from the results of thermo-couple measurements by V a a r t a j a (1949, 1950, 1954). These measurements indicated that maximum temperatures of 70° C occurred at forest sites where the mid-summer minimum remained below the freezing point. Altogether, six problems concerning the influence of climatic factors to seeds and seedlings were studied experimentally. In addition, an attempt was made to estimate the importance of various factors in several seeding experiments in the field in Finland. The purpose of the study was to give starting points to silvical studies, not to go into the physiology of the phenomena. The discussion is mostly limited to the results and references dealing with the tolerance of trees in seed and succulent seedling stages. The latter is considered as the earliest seedling stage according to the definition of B a k e r (1950).

Related studies are being carried out on shade tolerance and germination. A study on the diseases of seeds and young seedlings has already been published (V a a r t a j a, 1952).

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# Effect of temperature variation on dormant seed

Seed of *Pinus silvestris* was kept in warm incubators and in refrigerators in turn so that the temperature variation simulated the natural daily rhythm. The germination of seed pretreated in this way was tested.

The maximum temperature inside an exposed brown seed was found to be, on the average,  $2.s^{\circ}$  C higher than that in adjacent surface soil (V a a r t a j a, 1950). Both temperatures were the same, or that of the soil was even a little higher, in other similar comparisons. This discrepancy could be explained only partly by the differences in the conductivity errors and in the correction of this (V a a r t a j a, 1949). To study this problem further, the following investigation was made.

The junctions of a thin thermo-couple were inserted inside two seeds of *P. silvestris*. One seed was brownish-black (A) and the other greyish-white (B). On a very bright day (July 14, 1950) in Helsinki, temperature differences between the seeds were as follows ( $3 \times 20$  measurements, ° C):

1.	Both on white sand	$A - B = 1.9 \pm 1.0$
2.	Both on forest humus	$A-B = 3.0 \pm 1.6$
3.	B on humus, A on sand	$B-A = 4.2 \pm 0.9$

These results show that the maximum temperature of an exposed seed evidently is dependent on its color but still more dependent on the properties of the substratum. The maximum temperature inside a seed may apparently be a little higher or lower than the temperature in adjacent soil.

At night the temperature conditions are more balanced, and no marked difference is expected in minimum temperatures between seeds and substratum.

When the tolerance of seed was being tested, the seed was kept in asbestos boxes with water bottles to increase the thermal inertia. This provided gradual changes in temperature when seed was moved from refrigerator to incubator and back. The temperature of seed was checked by the thermocouple. The shape of daily temperature curves resembled that of exposed surface sand on a heath (V a a r t a j a, 1950; Fig. 2).

The quality of seed pretreated in this way for 5 days was immediately

tested by recording the germination for a period of 21 days. This was done on moist sterile quartz sand under diffuse light, the temperature alternating between + 23 and 25° C.

Two kinds of seed were studied. For one experiment (1 A) the seed was extracted from the cones under temperatures which did not exceed  $40^{\circ}$  C during the first moist phase and later  $50^{\circ}$  C. The cones were collected in mid-winter from healthy dominant trees in the center of a large *Calluna* heath at Hyvinkää in South Finland. For the other experiment (1 B) the mixture of commercial seed of three Finnish origins was used.

Expt. 1 A was repeated three times using 50 seeds in each treatment. In one part of the treatment the seed was allowed to imbibe water from a moist filter paper one day before and during the temperature treatments. In the other part, the seed was kept dry after the extraction.

The following average germinations of three replications were obtained from seeds pretreated in various ways:

	P r e t r e a t m e n t s		Germination, % of
	Temperature extremes,°C	Moisture	$\begin{array}{l} \text{treatments } e \text{ and } f \\ (\text{check} = 100) \end{array}$
a.	050	moist	16
b.	070	dry	29
с.	0-50	dry	65
d.	030	moist	94
e.	(20-25)	dry (check 1)	100
f.	0-1	moist (check 2)	100

The results of Expt. 1 B (dry treatments, 12 replications in each) showed a similar tendency: treatment c (0—50° C, dry) reduced relative germination to 86  $\pm$  3.0 % and treatment b (0—70° C, dry) to 72  $\pm$  2.9 %.

The reductions in germination were smaller in Expt. 1 B than in Expt. 1 A. Probably the seeds that were sensitive to heat had already lost their germination capacity in the commercial extraction process. Also the original heat resistance of seeds varies, for instance, from tree to tree (K a n g a s, 1942).

Somewhat similar treatment by S mith (1951, Table 7), but with smaller temperature amplitudes, reduced the germination capacity of *Pinus strobus* L. very little with dry treatment. Complete loss occurred under moist conditions. Seed of *P. strobus* also is susceptible to the extraction process of moist heat at  $50^{\circ}$  C (Rietz and Torgeson, 1927).

Evidently the extreme temperature variation that commonly takes place on exposed forest sites (S m i t h, 1951; V a a r t a j a, 1949, 1950, 1954) is to be considered as a factor affecting dormant tree seeds. The effective part of the process may be mainly the maximum and perhaps not the minimum temperatures.

# Heat tolerance of seedlings

Three kinds of experiments were conducted. The thermal death point of seedlings was determined by immersing them in hot water (Expt. 2 A). That temperature of exposed surface soil at which seedlings were injured was measured (Expt. 2 B). The incidence of heat injuries of two species on various artificial soils was compared (Expt. 2 C).

E x p e r i m e n t 2 A. Succulent *Pinus silvestris* seedlings were grown in pots of sand under following conditions: (a) in the laboratory under diffuse light at constant temperature; (b) at constant temperature at night, but with a four-hour exposure every day to heat from the sun and an electric radiator (at that time the temperature of the surface soil in pots usually exceeded  $40^{\circ}$  C). (c) conditions by day were the same as in (b), but at night the seedlings were out of doors and exposed to minimum temperatures of from -5 to  $5^{\circ}$  C.

These treatments lasted seven days. Then groups of the seedlings were immersed in water baths of seven different temperatures. A thermocouple was attached to the seedlings to show the exact temperature of water around them. When immersed, each five seedlings were surrounded by a small metal cylinder to eliminate the effect of cooler water currents.

The highest temperatures tested caused the immediate death and the disappearance of turgidity in seedlings. The result was not immediately clear after the treatments at lower temperatures. A survival was recorded only if no severe injury appeared when the tested seedlings were kept growing for a week. Table 1 shows the results.

Experiment 2 B. Hardened *Pinus silvestris* seedlings of late succulent stage were grown in shallow pots.

When the tests were made, the sandy bottom soil was moist and cool but the layer of 3 cm loose humus (mor powder) was dry and hot. Thermocouples were inserted carefully in the thin surface layer of soil at the base of seedlings. The pots were exposed to radiation from the sun and an electric heater so that the thermo-couples showed approximately  $50^{\circ}$  C.

Then the soil temperature at the base of a seedling was raised to a certain point for 5 minutes by concentrating the sun's radiation with a large magnifying glass. Discoloration or sometimes an immediate girdling of the stem appeared as a result.

6

Factors causing mortality of tree seeds and succulent seedlings

#### Olli Vaartaja

62.3

62.3

Table 1. Critical maximum temperatures for *Pinus silvestris* seedlings in hot water tests (temperatures at which both death and survival occurred among 20 seedlings after immersion for 15 minutes.<sup>1</sup>

Test Temperature ° C	Pretreatment				
	$\overset{\textbf{Shade}}{+\ 20^{\circ}\ \text{C}}$	Day: + 40° C Night: + 20° C	Day: $+40^{\circ}$ C Night: $-5$ to $+50^{\circ}$ C		
49.3					
51.5	$\times$				
53.5	$\times$		×		
55.5		×	×		
58.2					

The critical temperature of the surface soil for seedlings varied from 54 to  $65.5^{\circ}$  C. Some seedlings survived a soil temperature of  $64.5^{\circ}$  C; some died from injury at a soil temperature of  $61.1^{\circ}$  C; many were injured by soil temperatures of 54.0 to  $65.5^{\circ}$  C but recovered under favourable conditions. Probably these would have died with longer exposure to heat and other difficulties of field conditions. Exposure to a temperature of 57 to 58° C for 30 minutes is known to be as injurious to certain conifers as  $63^{\circ}$  C for 5 minutes (in immersion, L or en z, 1939).

Under the experimental conditions, large differences probably existed between surface soil and root collar temperatures. This difference is caused mainly by the fact that the stems of seedlings conduct heat to the cooler soil layers better than the soil itself and perhaps were also cooled by water rising in stems from soil to leaves. Thus the difference is large in case of low thermal capacity and low thermal conductivity of surface soil, and high thermal capacity of deeper soil. Such was the case in the experiment where surface soil was loose dry humus, and the deeper soil was moist compact sand.

Consequently, the exposed seedlings can survive a surface soil temperature as high as  $64.5^{\circ}$  C (in the above experiments) only on a dry humus cover which provides the most favourable conditions. On sandy soil, a soil temperature a few degrees lower may be fatal. The survival of an exposed seedling in the field was actually observed when the temperature of the surface humus was 59° C (July 5, 1949, at Ruotsinkylä, north of Helsinki).

To study the complications caused by the actually lower temperature

(V a a r t a j a, 1954) but more adverse thermal properties of sandy soil as compared with humus covered soil, Experiment 2 C was performed.

E x p e r i m e n t 2 C. Shallow metal containers were half-filled with moist fine silty sand and with a cover layer of various dry soils. The surface was made slightly concave to study the effect of differently exposed slopes. Twenty *P. silvestris* seedlings of the young succulent stage were planted in each container. These were exposed to strong insolation at a warm place each in a similar position. The first typical symptoms of heat injury appeared in a few hours in seedlings on the most exposed slope.

After two bright days the numbers of seriously injured seedlings on four different surfaces were:

a.	forest humus (mor) powder	19
b.	coarse quartz sand	17
с.	mixtures of humus and fine sand	13
d.	fine yellow sand	7

Most survivors were on a slope with northern exposure. Many of the rest were inclined southwards, thus shading their own bases. When the positions of containers were changed later, all the seedlings soon died or were seriously injured. The common symptom was discoloration and constriction at the base. A few seedlings showed enormously swollen stems.

The bottom soil remained moist long in all containers except that with silty sand (d). This suggests that the water rose more readily to the surface of fine silty sand than in other soils, which can be explained by the capillary properties of fine silty sand. The inertia effect of water on the temperature rise at the surface of fine silty sand evidently caused the low mortality in this soil type. The soils with a dry surface (a) and (b) showed nearly the same mortalities although they were otherwise quite different. The temperature of humus at the surface was obviously higher than that of quartz sand (V a a r t a j a, 1954). The similar mortality on these substrata suggests that the temperatures in the seedlings themselves must have been about the same or above the critical level regardless of the substrata.

When Experiment 2 B was repeated twice with one soil type and two species, no consistent differences were found between *Pinus silvestris* and *Picea abies*.

Similarly, M  $\ddot{u}$  n c h (1914) found that these two species were injured at the same temperature, namely 54 to 55° C within two hours' exposure in an incubator on moist sand. This temperature is also in accord with the results of the immersion tests described above (Table 1), although

<sup>&</sup>lt;sup>1</sup> In tests of 30 seconds at  $58.2^{\circ}$  C some of the hardened seedlings survived though slightly injured. In tests of 150 minutes at  $55.1^{\circ}$  C no seedlings survived.

62.3 Factors causing mortality of tree seeds and succulent seedlings

#### Olli Vaartaja

62.3

the seedlings in the present and in Münch's investigations represent rather different climatic races. Also the results with American species agree roughly with these. Exposure to temperatures between 49 to 58° C for 13 to 30 minutes in moist air killed young seedlings of *Pinus contorta* Dougl., *Pinus ponderosa* Laws., *Picea engelmannii* Parry, and *Pseudotsuga taxifolia* (Poir.) Britton (B a t e s and R o e s e r, 1924). Exposure of young seedlings of *Pinus resinosa* Ait., *Pinus strobus*, *Pinus banksiana* Lamb. and *Picea glauca* (Moench) Voss to 44 to 48° C for two hours was fatal in immersion (S h i r l e y, 1936).

In all of these experiments the differences in lethal temperatures between species have been small, only a few degrees C, especially where the same methods were applied. A few degrees' difference exists even between individuals, especially if the pretreatments, resulting in hardening, vary (Table 1). Other investigations (S a p p e r, 1935) have also suggested that hardening of some plants can increase their heat tolerance by a few degrees C.

S h i r l e y (1936) found that the stem of a seedling is more tolerant than the other parts. In immersion tests which provide the same temperature for all parts of the seedlings, however, this difference was mostly nil or very small, about 1° C (S h i r l e y, 1936; Table 4). Accordings to L o r e n z (1939) most cortical cells of the seedlings of some species tolerate 58° C when immersed for 10 minutes or longer. However, the normal function of a whole seedling may already be seriously disturbed at a lower temperature.

Although the immersion test is an exact means for comparative and physiological studies of heat tolerance of seedlings, the soil temperature associated with injuries also need attention. In general, a higher temperature in surface soil is required to produce heat injuries than that which is critical for the seedlings themselves (cf. results of Expt. 2 A and 2 B). As discussed above, this difference is dependent on the soil properties (p 8.). In Baker's thermocouple measurements (1929) this difference was 8 to 11°C. Daubenmire's (1943) thermocouple measurements showed Pinus edulis Eng. seedlings were able to tolerate a soil temperature as high as 70° C. This was at least partly caused by the thickness of cortical tissues and massiveness of the stem. The problem is further complicated by self-shading and ability to recover. Thus in Linteau's (1948) experiments the big seedlings of Betula lutea (Michx. f.) in the open suffered fewer heat injuries than the small seedlings under fairly dense canopy. The small morphological differences between young seedlings of Pinus silvestris and Picea abies were not sufficient to cause a marked difference in heat tolerance in Experiment 2 C. Further research is needed to determine the importance of all these factors.

The exposed soil cover of litter or humus is evidently dangerous for seedlings as indicated by Experiment 2 C and many field studies (e.g. H a i g, 1936; I s a a c, 1938; R u d o l f, 1938; S m i t h, 1951). It is doubtful whether fine, dry sand is a relatively safe soil, as suggested by Experiment 2 C where the sand became moist. However, to prove this may be difficult because of the complication by drought injury.

## Drought tolerance of germinating seed (Expt. 3)

Seeds of four tree species were germinated on quartz sand. When the radicles were from 5 to 10 mm long, the seeds were placed loosely on various moist soils in shallow pots and exposed to wind and insolation (August, 1950, in Helsinki).

Table 2 shows the results obtained in experiments on three soils as percentages of successful rooting recorded from those experiments during which clear rainless weather prevailed for five days.

 Table 2. Effect of temporary drought on rooting of germinating seeds (in pots in Helsinki, August, 1950; 100 to 120 seeds in each individual test).

	Successful rootings in five days, $\%$				
Substratum	Pinus silvestris	Picea abies	Betula verrucosa and B.pubescens		
Humus (mor)	1.5 $(0-7)^{1}$	2.4 $(0-20)^{1}$	0		
Coarse sand	0	1.s (0-20) <sup>1</sup>	0		
Fine silty sand	0	$1.2 (0-20)^{1}$	0		

In spite of the plentiful moisture in the soils, at least in deeper layers, radicles only seldom succeeded in penetrating the soil and soon withered. Any unevenness on the surface seemed to favour rooting.

The variable results and average superiority of *Picea abies* could not be explained. This climax species was exepted to be less drought-tolerant than pine (cf. also Table 3 and Figs. 1 and 2).

In another series of experiments on sand, each seed was loosely covered by a small leaf of *Vaccinium vitis-idaea*. This protection was not sufficient to increase rooting incidence materially. The rooting percentage was

<sup>1</sup> Range between replications.

10

62.3 Factors causing mortality of tree seeds and succulent seedlings

#### Olli Vaartaja

62.3

higher (pine 22, spruce 27) in a third series carried out at the south-eastern window of the laboratory on sand.

When testing a substratum of moss mixed with lichen (mostly *Callier-gonella schreberi* and *Cladonia* spp.), some rainfall always occurred. Hence, the following results obtained are not fully comparable with those above:

S pecies	Average rooting %
Pinus silvestris	16
Picea abies	17
Betula pubescens Ehrh	49
B. verrucosa Ehrh	16

Probably both the chance rain and the uneven protecting surface contributed to this frequent rooting on moss and lichen.

The poor rooting ability of the four species on even surfaces was probably due to their poor drought tolerance in this early stage.

Other studies have indicated the high susceptibility of *Pinus silvestris*, *Picea abies* (R o h m e d e r, 1951), *Pinus taeda* L., and *Liquidambar styraciflua* L. (B o r m a n, 1953) to drought just after germination. Field observations (e.g. L e B a r r o n, 1944) have also shown the importance of drought injuries in this stage.

#### Drought tolerance of seedlings

Two methods were used. The survival of seedlings of four species was studied after these had been kept for a period without water in the laboratory (Experiment 4 A). A similar experiment (4 B) was conducted on an open field where the effect of rainfall was avoided by means of glass covers.

E x p e r i m e n t 4 A. Twenty to forty germinating seeds were planted in zinc pots filled with various soils, shown in Table 3. The pots were kept in the laboratory by the window. The seedlings were exposed for half the day to light of an intensity that was 50 % of that usual in Helsinki in August and September. In addition, fluorescent tubes provided long photoperiods. The temperature was from 17 to 25° C. The pots were watered daily to maximum capacity. In each pot five wheat plants were also planted to make the drying of the soil even. They also served as moisture indicators in each pot, since the first wilting symptoms of wheat leaves are often clearly visible. The surface of each pot was covered thinly with coarse quartz sand to slow down the drying of soil. Each pot was inoculated with forest humus to decrease the danger of damping-off. After the tree seedlings were well rooted, the watering of the pots was stopped. It was begun again 21 days after the wheat leaves showed the first clear drought symptoms. Survival was recorded after the seed-lings had had an opportunity to recover from the drought.

Table 3 shows the results. The seedlings passed the succulent stage before they began to die.

Table 3. Drought tolerance of seedlings. (Pot experiments with wheat indicators in laboratory. Helsinki, 1950.)

S o i l	Species	Number of seedlings	Average exposure of each soil, days	Survival after 21 days from the wilting signs of indicators, %
Coarse	P. silvestris	25		0
				0
quartz	Picea abies	25		0
sand	B. verrucosa	25	57	4
	B. pubescens	25		0
Fine	P. silvestris	40-39		5 and 8
sand	Picea abies	40-39	53	0
	B. verrucosa	21 - 38		5 and 8
	B. pubescens	40 - 40		0
Forest	D. cilvasteis	20 00		
	P. silvestris	38-22		0 and 24
humus from	Picea abies	23 - 39	77	0 and 5
Myrtillus	B. verrucosa	24 - 40		0 and 15
type	B. pubescens	25 - 40		0

The difference between soils was marked. Humus (mor) remained above the critical moisture level much longer than sandy soils. The difference between fine sand and coarse quartz was small and perhaps insignificant. Probably the high water retaining capacity and hence large initial amount of water contributed to the good results on humus as compared to quartz. Fine sand dried readily owing perhaps to the rapid capillary movements of water in this soil type. Similarly, A u e r (1948) found that young seedlings of *Larix europaea* tolerated drought longer in raw humus layer than in sandy soils. On the other hand, the wilting took place at a higher water content in humus than in sand. In B a r r's (1930) greenhouse experiments the seedlings of *Picea engelmannii* survived a little longer in humus than in sand or clay.

So far as the data allow comparisons between the species, the differences between them seem to be in accord with their site require-

12

15

62.3

62.3

ments. The apparently least tolerant species, *Betula pubescens*, occurs mostly on fresh, moist, or wet sites. The most tolerant ones, *Pinus silvestris* and *Betula verrucosa*, have a wide ecological amplitude but commonly occur on very dry sites. *Picea abies* is an intermediate species both in the above results and in general occurrence, occupying mostly fresh or moist sites.

In replications made under natural photoperiods in the fall, birches and wheat indicators did not develop properly. Survivals of pine and spruce after 56 days' exposure were (%):

This again illustrates the importance of the soil.

Experiment 4 B. Twenty germinating seeds were planted in glass containers filled with fine silty sand (subsoil) or forest humus (mor) from a mixed stand of *Myrtillus* type. Three moistures were used: »Dry», the original low moisture of soils; »Wet», moistened to the full capacity; »Moist», moistened to approximately the mid point by weight between these two. These original differences in moisture were hardly noticeable after the containers had been unwatered for 30 days.

The containers were kept inserted in soil on an open field. The soil surfaces were left bare. Some of the pots were protected with a sheet of glass supported a foot above the seedlings. Because of drought, however, all the containers were in the same position with regard to rain. The difference in transpiration conditions between exposed and protected containers is shown by the average evaporation rates from small dishes on the ground:

The mortality rate in fine silty sand soil is shown by Figs. 1 and 2. In humus (mor) soils the mortality (pines under glass only) was at first similar to that in sand as is seen in Figs. 1 and 2, but lower later on. Soil differences caused finally differences in mortality as shown by the following percentages at the end of the experiment in humus:

Dry	Moist	Wet	
26	53	66	

Again, as in Experiment 3 (germinating seeds), humus was generally a better substratum than fine silty sand, and spruce was more tolerant



Fig. 1. Mortality of fully exposed seedlings. Initial soil moisture at three different levels.



Fig. 2. Mortality of seedlings under glass cover. Initial moisture at three different levels.

3

20

2

62.3

62.3

than pine in the early stages. Similarly, Fabijanovsky (1950) found *Picea abies* to tolerate drought a little longer than *Pinus silvestris* in their early seedling stage.

In later stages the situation was more complicated. The good start of spruce continued only under the protection of glass. On being fully exposed, all spruces suddenly died, though a few pine remained alive. This was to be excepted, considering the ecological distribution of these species on various sites.

The bare surface soil dried much earlier than in Experiment 4 A where quartz sand protected the soils. This may explain the difference in the results between Experiments 4 A and 4 B.

All seedlings that died had a short root system, the tap root not exceeding 35 mm. Probably the seedlings were already injured in an early stage. The survivors, on the other hand, grew deep roots surprisingly soon. The most vigorous seedlings finally produced a tap root over 75 mm long. They grew a root of 70 mm in a month.

The development of the seedlings is illustrated by the following figures showing the dry weights of seedlings grown for 4 weeks under cover (mg):

Original	Pinus	silvestris	Picea abies
noisture of	humus	fine sand	fine sand
Wet	 $11.8 \pm 1.0$	$10.1 \pm 0.6$	$8.1 \pm 0.7$
Moist	 $7.7 \pm 1.0$	$9.0 \pm 0.6$	$8.7 \pm 0.7$
Dry	 $5.8\pm0.4$	$(6.6 \pm 0.7)^{1}$	

The figures illustrate the well-known, slow growth of young *Picea abies*. This may be an explanation to its drought resistance becoming lower in a later seedling stage, as compared to *Pinus silvestris*.

When the experiment was repeated during September and October, moist weather periods occurred. No mortality took place even under glass where seedlings survived longer than 60 days without getting water to soil. The average evaporation rate was 2 mm/day under glass.

The results of Experiments 4 A and 4 B (Figs. 1 and 2) stress the importance of the early stages in drought injuries as is already suggested by Experiment 3. Later on, the seedlings may often escape drought injury if they are vigorous enough to develop deep roots. This was also the case in the field experiments described later (7 A, B). Root development to escape soil drying has been found to be an important factor in the survival of several tree species in regeneration studies (H a i g, 1936;

LeBarron, 1944; Linteau, 1948). This aspect of the drought resistance of seedlings is often more advantageous than physiological drought resistance, which, generally speaking, is linked with dormancy (Shirley, 1939) and is antagonistic to growth.

K a r s c h o n (1949) found that Swiss seedlings of *Pinus silvestris* and *P. montana* Mill. (= *P. mugo* Turra) tolerated drought under long than short photoperiods more successfully. He studied very young succulent seedlings. In that stage, drought tolerance may depend primarily on the root development and growth rate, which are favoured by long photoperiods. Later drought tolerance is determined also by cortex formation, root-top ratio (Wilde and Voigt, 1949) and physiological resistance (Shirley and Meuli, 1939). Karschon found *P. montana* a more tolerant species than *P. silvestris*.

# Transpiration tolerance of seedlings (Expt. 5)

Young succulent seedlings grown on quartz sand were transplanted to shallow pots filled with fine sand with forest humus inoculum (from *Myrtillus* type). The pots were kept in sunny laboratory windows in Helsinki in the summer of 1950 at 20 to  $25^{\circ}$  C. A week after planting the pots were exposed to an air current from a strong fan during the day for 4 or 6 weeks. This caused high transpiration from those pots nearest the fan. The transpiration conditions were studied by measuring the evaporation rate from small glass dishes placed among seedlings in each pot. By frequent watering, soils were kept moist in all pots. The experiments were repeated eight times with four species (*Pinus silvestris, Picea abies, Betula verrucosa*, and *B. pubescens*).

Except for a few seedlings that apparently were rooted poorly and fell over, all seedlings survived in the experiments. However, the growth rate was affected by four evaporation conditions as is shown by the following dry weights of 30 pine seedlings after six week's exposure:

	Evaporation mm/day:			1
	6.7	4.3	3.0	1.7
Mean weight, mg	12.85	13.60	14.35	15.07
Standard error of weight, mg	$\pm$ 0.52	+ 0.60	± 0.47	± 0.49
Approx. increase during exposure	5.8	6.6	7.7	8.1

Although seedlings of the same size were selected carefully when beginning this experiment, some small random deviations could not be avoided. This and the inherent individual differences must have increased

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<sup>&</sup>lt;sup>1</sup> Seedlings died just before the end of the experiment; otherwise only seedlings which remained alive were weighed.

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the standard errors shown above. Still the weight difference between the results of the lowest and highest evaporation rates,  $2.22 \pm 0.72$  mg, is statistically significant. The effect of transpiration conditions was highly probable.

The results of some other weighings yielded still larger standard errors and no statistically significant differences between the treatments. It was evident only that the other three species also underwent some growth even under the most unfavourable transpiration conditions.

The results of this experiment show that transpiration conditions are not a pathological factor if the seedlings are well rooted in moist soil. The same was found in D a u b e n m i r e's experiments (1943) with 6 conifers from the Rocky Mountains. This does not mean that extreme transpiration conditions were without importance; they often cause the exhaustion of water from soil as, for instance, in Experiment 4 B (Figs. 1 and 2). Thus in S a t o o's experiments (1948) with the seedlings of *Robinia pseudoacacia* L., the growth was affected by strong wind much more if soil moisture was deficient. However, the seedlings survived an average wind of 3.6 m/sec during four weeks even when soil moisture was moderately low.

#### Cold (frost) tolerance (Expt. 6)

Potted seedlings were grown in a mixture of sand and *Sphagnum*-humus with a little inoculum of forest humus (from *Myrtillus* type). Before exposing to cold the seedlings were kept under various light conditions at 17 to  $22^{\circ}$  C.

Seedlings were tested against gradually falling temperatures by keeping the pots overnight in a refrigerator. Strong ventilation kept the temperature uniform inside the refrigerator. The minima were recorded by minimum thermometers.

After testing the lots of seedlings in various temperatures from -3 to  $-11^{\circ}$  C, the seedlings were allowed to warm slowly. Then they were kept in the laboratory for observation of symptoms. If the stem or more than half of the leaves withered, the injury was considered fatal. If 10 % or more of the seedlings were fatally injured, a lethal minimum temperature was recorded. Each test consisted of from 30 to 100 seedlings of each species.

The results were inconsistent concerning the early succulent stages. The seedlings passing or past this stage showed more indicative results (Table 4). No clear differences were found between 2 photoperiodic pretreatments (10 and 24 hours). Therefore all the data are grouped only to the species and two developmental stages. As a whole the order in cold resistance of the species corresponds to the order in sociological succession. The pioneer species *Alnus incana* (L.) Moench was the most susceptible. *A. glutinosa* Gaertn. differs from the others in that it is a species which usually grows on wet sites.

The damage to some pine individuals at  $-3^{\circ}$  C (of different photoperiods) was unexpected considering the pioneer character of the species and the good resistance of other individuals. The test results suggest that the ecological amplitude of this species may be wider than it is commonly accepted. In fact this species regenerates even under those rather dense canopies (V a a r t a j a, 1951) where the nocturnal minima are a few degrees higher than in the open (V a a r t a j a, 1950, 1954).

Table 4. Survival and lethal temperatures for certain tree seedlings. (No previous hardening; overnight tests in pots in refrigerator; Helsinki, July 1951.)

Stage of seedlings <sup>1</sup>		Species	Highest lethal minimum, ° C	Lowest survival minimum, ° C
Height growth continuing	•	Alnus incana Pinus silvestris Picea abies A. glutinosa	5 3 3 above 3	below — 7 below — 10 above — 6 — 7
Height growth ceased		Pinus silvestris Picea abies	-3 -10	below — 11 — 10

The sensitiveness of *Picea abies* to early frosts is well known (M u l t am ä k i, 1942). However, Table 4 shows that the resistance of this species is very different at different stages. R o h m e d e r (1951) found that even a few days' difference in the age of *Fagus silvatica* L. seedlings made a difference in cold resistance. The cold tolerance of young seedlings of many tree species is dependent on the photoperiods and the minerals available, but in different ways in different species, and also in their different stages (S a t o and M u t o, 1951). The question of cold tolerance is very complicated, if also hardening is considered (see the review by L e v it t, 1948).

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<sup>&</sup>lt;sup>1</sup> Tests with very young seedlings gave varying results; in general the critical temperatures tended to be higher than the above.

<sup>&</sup>lt;sup>2</sup> All spruce seedlings grown in low light intensity (2 %) survived.

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### Factors causing mortality of tree seeds and succulent seedlings

#### Seedings in field

Seedings were made on five different forest sites that represent the most important forest types of South Finland. The check against birds, which were unexpectedly destructive, was insufficient and most of the experiments give information only on the factors affecting the dormant life of the seeds.

Experiments A and B. Seeding experiments were carried out near Hyvinkää aerodrome in South Finland. The method was the one commonly practiced in Finland. A patch,  $30 \times 20$  cm, was denuded to sand. In the middle of this a furrow was pressed in firmly. Into the furrow, exactly 20 seeds of especially good quality were sown, June 8, 1950. The furrows were of various depths and the seeds were covered with twigs or sprinkled with various powdered materials to a depth of from 5 to 40 mm (Table 5). Each treatment was repeated 13 times on a fine sandy soil (7 A) and 5 times on a gravelly soil (7 B). Table 5 shows the main results.

# Table 5. Effect of cover and of depth of seeding furrow (fine sandy and gravelly heaths of *Calluna* type in South Finland, 1951).

		Kinds of	Survival after one year, % <sup>1</sup>		Mortality, 😤 ²			
No. Depth of furrow cm	Sand				Gravel			
	cover	Sand	Gravel	Summer	Fall & Winter	Summer	Fall & Winter	
1	1.5	Birch twigs	33	5	27	5	73	8
2	1.5	Sand	50	16	6	12	25	31
3	1.5	OMT humus	49	19	7	1	26	25
4	1.5	VT humus	56	33	6	6	21	8
5	1.5	Cladonia	48	32	11	4	2	20
6	1.5		51	30	10	0	7	27
7 a	3-4	Sand	40	40	8	8	5	3
7 b	2	Sand	61	51	13	2	2	5
7 C	1	Sand	50	24	19	3	0	2
7 d	0.5	Sand	26	12	0	25	0	24

<sup>1</sup> As percentage of the number of seeds sown.

<sup>2</sup> As percentage of of the maximum number of seedlings observed in each spot.

The following differences in the results (survivals) on the sandy site were statistically significant:

Plots	Difference $\pm$ standard error, %									
A. Between cover treatments										
Plot 4 (VT humus) — Plot 1 (birch twigs)	$=~23\pm7$									
Plot 6 (no cover) — Plot 1 (birch twigs)	$=$ 18 $\pm$ 6									
Plot 2 (sand) — Plot 1 (birch twigs)	$=$ 17 $\pm$ 7									
Plot 3 (OMT humus) - Plot 1 (birch twigs)	$=~16\pm7$									
B. Between furrow depths										
Plot 7 b (2 cm) — Plot 7 d (0.5 cm)	$=$ 35 $\pm$ 8									
Plot 7 c (1 cm) — Plot 7 d (0.5 cm)	$=$ 24 $\pm$ 7									
Plot 7 b (2 cm) — Plot 7 a (4 cm)	$=$ 21 $\pm$ 8									

The data for gravelly soil showed similar tendencies as those for sandy soil. However, the differences were more pronounced and the general level of survival was lower. This suggests that the same factors were working on both soils but more critically on gravelly than on sandy soils.

After three growing seasons there still were about the same ratios in survivals between the treatments. However, the differences were no longer statistically significant probably due to the increased variation in each treatment. The same was true concerning the dry weight of seedlings. Some seedlings of the OMT humus (mor from a stand of Oxalis-Myrtillus type) treatment were very vigorous. The dry weight of a threeyear-old seedling from this treatment was 728 mg while the smallest ones of various other treatments weighed only from 15 to 30 mg. The treatment by Cladonia powder seemed to produce the smallest seedlings, but these had a fairly good survival. The weights of the largest seedlings of this treatment averaged on sandy soil and on gravelly soil, 59 to 65 per cent respectively of those treated with OMT humus. Though not statistically significant, this difference may not be accidental because of the probable difference in fertilizing values of Cladonia powder and OMT humus. VT humus (mor from a stand of Vaccinium type) seemed to have an intermediate effect.

The effects of *Cladonia* were in agreement with the results of greenhouse experiment with lichen by L e i b u n d g u t (1952).

In general, the seeding results were good in spite of prolonged severe drought during a part of July and the whole of August in the first growing season. The seeding spots that failed to produce a single seedling were isolated exceptions in nearly all treatments. Only the treatment with birch twigs was inferior.

Olli Vaartaja

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A heavy rain just after sowing caused prompt germination. The water carried sand and litter and thus the germinating seeds were covered even in the control treatment where the seeds were not intentionally covered. As a result no heat or drought injury could be detected with certainty. Low germination in the treatment with a shallow furrow was obvious and can hardly be accredited to any other factors but the temperatures of the loose soil surfaces. Once established, the seedlings of these plots survived well during the summer.

A fatal factor was the conspicuous injury by snails and, perhaps, insects. These ate the cotyledons of many seedlings. This factor caused some mortality irregularly on various spots, and high mortality where birch twig cover was applied.

The role of the twigs in the damage could not be discovered. Perhaps they carried polyphagous animals to the seed spots or the twigs in otherwise dry and poor environment attracted animals to the spots. It is also possible that birch is the usual host plant of the animals and after the birch twigs dried, pine was used as a secondary host. In any event it cannot be concluded that fresh twigs are generally a detrimental cover for seed furrows. Fresh twigs offer the possible advantage of shading the furrow more at first during the germination phase but less later after becoming dried and shrivelled.

The mortality during autumn and winter was caused mostly by frost heaving, which broke roots of seedlings or pulled them from the soil.

The majority of the seedlings became discolored in midsummer or fall, showing lilac, brownish, or yellow needles. The incidence of discoloration could not be correlated with the type of treatment. Probably most of the discoloration was caused by the hardening processes. The most discolored seedlings grew very slowly. Fungus diseases were of no importance in the seedings.

Though litter accumulation probably offered beneficial protection during the germination phase, it was too heavy in the later phases. Many of the deeper seed furrows became gradually covered by pieces of bark or twigs and lichen after the action of rain and wind, so that only the tips of the needles appeared over the litter accumulation. This must have been harmful to the growth of the seedlings. On the other hand, since litter accumulation protected from frost heaving, the optimum cover thickness seemed to be from 1 to 2 cm. Because nearly the whole depth of a seeding furrow tends gradually to become filled by litter, furrows exceeding a depth of 3 cm should be carefully avoided especially when there is heavy litter in the vicinity. On gravelly soil (Experiment 7 B) some seedlings were covered through the action of frost heaving in soil and, in a few cases, of a beetle, *Broscus cephalotes* L. Probably this insect also cut seedlings.

The soil moisture of the seeding site (7 A) was studied by the gypsum block method (B o u y o u c o s and M i c k, 1941). A resistance meter with radio oscillator of 100 cycles per sec and Wheatstone bridge was found to be simple to operate and to give satisfactory accuracy. However, as the moisture did not appear critical to the seedlings, the recordings were not calibrated to give available moisture of the soil. Still the recordings showed a silviculturally interesting feature. Ten blocks were inserted to a depth of six inches inside the seeding site where all birch and spruce saplings and young trees were eradicated. Ten other blocks were inserted similarly in an area where the trees were allowed to grow sparsely; they were located 10 to 15 m from both sides of the seeding spots. The results showed that the soil without these trees was always moister, on the average, than that with small trees left. When digging the soil, tree roots were found to penetrate everywhere, growing for distances several times the height of the trees.

Such experiments as 7 A and B should be repeated in some season when germination is not favoured by immediate rain, to determine if greater difference due to covers might appear. However, the furrow itself gives similar protection as the cover. Several thermocouple measurements in surface soil of fresh furrows always showed lower maximum temperatures than in adjacent looser soil. The difference was often from 5 to 11° C.

The depth of cover that seemed most favourable agrees with the results of Dengler (1925). In those seedbeds in his experiment which received plenty of water, the cover of only 0.5 cm with sand, clay, or humus was the best and a 2-cm cover was too thick.

E x p e r i m e n t 7 C. A seeding was made on an exposed dry heath in the vicinity of Experiment 7 A, May 4, 1951, soon after the snow had melted away. Various large mounts (500 to 5 000) or seed of six Finnish tree species were sown on each of 10 quadrats of 1 sq. m. Vegetation and soil cover were left undisturbed. No successful germination was detected until the middle of June. The germination percentages were (July 26): *Pinus silvestris* 0.14 and *Picea abies* 0.11. *Larix sibirica* Led., *Betula verrucosa*, *B. pubescens*, and *Alnus incana* did not germinate at all.

This low germination is in clear contrast to that in Experiments 7 A and 7 B with seed furrows and denuded patches (Table 5), and confirms the results of similar earlier seedlings (Hertz, 1934; Sjöström, 1947; Vaartaja, 1950).

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Evidently the exposure to extreme microclimate delayed and reduced the germination. Again (cf. V a a r t a j a, 1950), the unbroken patches of vigorous moss and lichen were inferior (germination approx. 0.001) as compared to the patches with weak or broken lichen. Some mortality occurred in a very early stage soon after germination, owing to heat or drought. Also, birds ate much of the seed though many ungerminated seeds could still be detected on July 26.

E x p e r i m e n t 7 D. On the same heath as was used for experiments 7 A, B, and C, but under pine canopy, 20 seed spots were denuded to humus. Fifty seeds of *Pinus silvestris* were sown in each, May 4, 1951. Germination was delayed during dry weather and before the moist season began, all seed was eaten by birds.

Experiment 7 E. An experiment similar to 7 D was carried out under a dense birch stand of *Oxalis-Myrtillus* type in Helsinki. Half of the seed patches were protected by screens. The seed was sown July 9, 1951. It rained the next night and prompt germination resulted: 23 % under screens and 16 % in unprotected spots. Birds ate some of the seeds and also damaged cotyledons of young seedlings to which the empty seeds were still attached. Some of the seeds were carried away by ants (*Formica rufa* L.). After a year the survivals were only 0.8 and 0.5 %. Probably most of the seedlings had been destroyed by fungi (V a artaja, 1952). Some seedlings were bitten by insects. The beetle, *Strophosomus rufipes* Steph., which is known to attack seedlings, was present on the plots. During the second summer *Lophodermium pinastri* (Schrad.) Chev. seemed to cause needle cast on seedlings.

 $E \ge p = r i m = n t 7 F$ . A similar experiment to 7 D was made on a very fertile site (*Oxalis-Majanthemum* type) under a dense spruce stand in Helsinki. No germination took place. Only two weeks after sowing most of the seed had been eaten by birds or carried away by numerous ants (*Formica rufa*).

E x p e r i m e n t 7 G. A similar experiment to 7 C (with plenty of seed of 6 species on natural soil cover) was made on the same site as 7 F. Some of the quadrats were protected by DDT from insects and by screens from birds. However, some small birds penetrated the screen openings of 20 mm and soon ate the seed. The remainder, which were unprotected, were destroyed by the numerous ants and perhaps by beetles. Two species of destructive *Otiorrhychus* beetles (F o r s s l u n d, 1941) were seen at seed spots.

The factors influencing seeding results or forest regeneration cannot be fully discussed here. The extremely varying results above stress the importance of environmental variety and the value of proper cultural methods, at least if associated with beneficial weather conditions, mainly with rains (for Experiments 7 A, 7 B, and 7 C). The great advantage from rains, even in the rather humid climate of Finland, is also suggested by other studies (S a r v a s, 1944; V a a r t a j a, 1950).

The Experiments 7 A to G as a whole show that the earliest phase is of special importance in the life of trees. They also show that some biotic factors can have a decisive role in this phase, especially on fertile sites if germination is delayed.

Well established seedlings tolerated drought better than is commonly assumed, as shown also by Experiments 7 A and 7 B.

#### Summary

Seed of *Pinus silvestris* was subjected to temperature variations which simulated those on exposed forest sites. This seed lost some of its germinative capacity during five days' treatments. Succulent seedlings of P. silvestris died when subjected to immersion for 15 minutes at temperatures from 51.5 to 55° C. Hardening pretreatments shifted the critical point 2 or 3° C upwards. In artificial humus soil exposed to strong insolation for 15 minutes, temperatures that were critical to the seedlings varied from 54 to 65° C. These temperatures were recorded by thin thermocouples in a thin surface layer of the soil. In natural conditions even somewhat lower temperatures may prove fatal. The exposure of succulent seedlings of P. silvestris and Picea abies to insolation on different artificial soils showed that most damage occurred on humus, quartz sand, and humus-sand mixture; moisture readily rising to the surface of fine sand reduced the danger of heat injury on this soil. Seeds of Pinus silvestris, Picea abies, Betula verrucosa, and B. pubescens tolerated exposure to drought very poorly if germination was advanced enough to show a radicle 5 to 10 mm long. The birches seemed to be less tolerant than the conifers. Fine sand was the most unfavourable and moss the most favourable substratum of those tested. When succulent seedlings were exposed to drought for 53 to 77 days in the laboratory, survival was much better in humus than in fine silty sand. Another experiment performed under two different conditions in the field showed similar dependence on soils. High mortality occurred in early stages. Picea abies tolerated drought

24

Olli Vaartaja

62.3

better than *Pinus silvestris* in early stages; later the relative tolerance was complicated by the conditions. Extreme transpiration conditions did not damage the young seedlings of *Pinus silvestris*, *Picea abies*, *B. verrucosa*, and *B. pubescens*, if the soil was moist; the growth, however, was reduced. Tolerance to cold of seedlings of each of the species *Pinus silvestris*, *Picea abies*, *Alnus incana*, and *A. glutinosa* varied considerably, especially with the developmental stages. In general, all these experiments indicated the sensitiveness of the earliest stages of trees. Many problems showed complex nature and need much additional research.

Seeding of *Pinus silvestris* in furrows pressed firmly on denuded spots yielded high germination after rain. The survival was high despite prolonged severe drought and the dry appearance (*Cladonia* cover) of the sites. Frost heaving and snail and insect injuries caused some mortality to seedlings. Germination was low in the shallowest seeding furrows due to higher temperatures. Other seeding of several species on natural covers or on humus gave poor results. The most important damaging factors, birds and ants, operated before germination, which was largely delayed by dry weather. Some loss was attributed to drought or high temperature soon after germination. The complexity and variability of factors affecting forest regeneration and the importance of the earliest phase of this is emphasized.

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### Puiden siemeniä ja sirkkataimia tuhoavista tekijöistä

#### SELOSTUS

Ne ekologiset tekijät, jotka vaikuttavat metsänuudistuksen aikaisimmassa vaiheessa ovat erittäin puutteellisesti tunnettuja. Puiden siemenet ja sirkkataimet elävät n.s. mikroympäristössä, jota vasta viime aikoina on alettu tutkia. Patologisestikin vaikuttavat tekijät ovat niin moninaisia ja vaihtelevia, että laajoja tutkimuksia erilaisissa oloissa tarvitaan ennen kuin niiden merkityksestä ollaan selvillä. Lähtökohtana tällaisille tutkimuksille voidaan pitää mikrokliiman selvittelyä sekä siementen ja tainten reagointia ääreviin ilmastotekijöihin.

Täydennykseksi aikaisemmin tekemiini metsiköiden mikroilmaston kuvauksiin (V a a r t a j a 1949, 1950, 1954), olen käsillä olevassa työssä tutkinut kokeellisesti eräitä puolia puiden siementen ja tainten kuumuuden-, kuivuuden- ja kylmänkestävyydestä. Olosuhteiden pakosta<sup>1</sup> tutkimukset muodostuivat luonteeltaan alustaviksi silti kartuttaen perin puutteellista tietouttamme ja toivottavasti antaen pohjaa vastaisille tutkimuksille.

Näihin tutkimuksiin läheisesti liittyvä työ valotekijöiden ja tuhosienien merkityksestä on julkaistu aikaisemmin (Vaartaja 1952) ja eräitä kesken jääneitä, siementen itämistä selvitteleviä kysymyksiä tutkin edelleen. Laboratooriokokeiden lisäksi suoritettiin eräitä kylvökokeita erilaisissa metsiköissä Etelä-Suomessa.

Siementen kuumuudenkestävyys. Kokeissa, joissa männyn siementä käsiteltiin karikkeen ja pintaturpeen ääreviä lämpötilavaihteluja jäljitellen (maksimi 50–70°), siemen menetti jonkin verran itämiskyvystään. Samoissa lämpötiloissa kuiva siemen sieti käsittelyn paremmin kuin kostea siemen. Kaupallinen siemen menetti vähemmän itämiskyvystään kuin siemen, joka oli karistettu alhaisessa lämpötilassa.

Taimien kuumuudenkestävyys. Kun männyn sirkkataimia upotettiin vesihauteisiin, joiden lämpötila mitattiin termoelementillä, havaittiin seuraavaa: 15 minuutin käsittely tappoi osan taimista, kun lämpötila oli 51.5 tai  $53.5^{\circ}$ . Karaistumista edistävät esikäsittelyt (7 vrk) lisäsivät taimien kuumuudenkestävyyttä niin että kriitillinen lämpötila oli 53.5 tai  $55.5^{\circ}$  (taul. 1).

Kun keinotekoiseen humuspintaiseen maahan istutetut männyn sirkkataimet pantiin 15 minuutiksi alttiiksi voimakkaalle säteilylle (aurinko + sähkölämmitin), vaurioituivat ne pintamaan lämpötilan ollessa 54—65°. Nämä lämpötilat mitattiin termoelementillä aivan ohuessa humuksen pintakerroksessa. Metsässä jonkin verran alhaisemmatkin pintamaan lämpötilat ovat tappavia. Kokeissa, joissa sirkkataimia kasvatettiin erilaisessa maassa auringon paahteelle alttiina, paistevauriot olivat lievemmät hiedalla kuin kvartsihiekalla tai humuksella. Tähän oli syynä veden kapillaarinen nousu hiedan pintaan. Kuusen ja männyn alttiudessa paistevaurioille ei havaittu merkittäviä eroja.

Itävien siementen poudankestävyys. Siemenet, jotka olivat kehittäneet 5–10 mm pitkän sirkkajuuren, kestivät poutaa huonosti. Melkein kaikki kuusen ja männyn siemenet ja kaikki koivun siemenet kuolivat oltuaan 5 vrk alttiina auringon paisteelle ja tuulelle. Sammal oli edullisempi itämisalusta kuin hiekka.

T a i m i e n p o u d a n k e s t ä v y y s. Osa nuorista puun taimista, joita kasvatettiin ruukuissa laboratooriossa, säilyi elossa ilman kastelua yli 53 vrk hiekassa ja yli 77 vrk humuksessa (taul. 3). Kuusen, männyn ja raudus- sekä hieskoivun kuivuudenkestävyydessä havaittiin vähäisiä eroja. Toisessa samanlaisessa kokeessa ulkona taimet jälleen kuolivat aikaisemmin hiekassa kuin humuksessa. Kuusi oli yleensä kestävämpi kuin mänty, mutta myöhemmin kuusen kuivuudenkestävyys riippui ratkaisevasti haihduntaoloista (kuvat 1—2); kuusen taimet eivät kasvaneet tarpeeksi nopeasti voidakseen mukautua vaikeisiin haihduntaoloihin. Nopeasti leviävä juuristo (7 cm kuukaudessa) auttoi parhaita männyn taimia kestämään 30 vrk:n pitkän poudan ja vaikeat haihduntaolot (5.5 ja 6.7 mm/vrk).

Taimien haihdunnankestävyys. Kaikki männyn, kuusen, hieskoivun ja rauduskoivun sirkkataimet säilyivät elossa vaikeissa haihduntaoloissa (6.7 mm/vrk), kun maa pidettiin kosteana. Eräissä kokeissa männyn taimien kasvu oli selvästi haihduntaoloista riippuvainen.

Taimien (hallan) kylmänkestävyys. Tulokset alustavista kylmänkestävyyskokeista näkyvät taulukossa 4. Yllättävästi eräät mänty-yksilöt osoittautuivat aroiksi äkillisille alhaisille lämpötiloille.

Kylvö kokeita. Useimmat viidestä, erilaisissa oloissa suoritetuista kylvökokeista antoivat erittäin huonon tuloksen. Kuivuus myöhästytti itämistä ja linnut sekä hyönteiset söivät siemenen. Ainoa poikkeus oli männyn vakoruutukylvös, jonka tulokset näkyvät taulukossa 5. Tässä kokeessa tutkittiin erilaisen vaon syvyyden ja peittämisen vaikutusta. Kaksi cm syvä vako osottautui paremmaksi kuin 0.5 tai 4 cm syvä vako. Vaon peittäminen koivun oksilla antoi huonon tuloksen hyönteis- ja etanatuhojen vuoksi. Itäminen oli hyvä vakoruutukokeessa pian kylvön jälkeen sattuneen sateen vaikutuksesta. Hyvin alkuunpäästyään taimet selvisivät ilman vakavia kuivuusvaurioita toista kuukautta kestäneen poutakauden yli, vaikka kasvupaikat olivat aukeita *Calluna* tyypin kankaita.

62.3

<sup>&</sup>lt;sup>1</sup> ASLA-stipendin saaminen ja muut tutkimustyöt Metsäbiologisessa Osastossa Kanadassa keskeyttivät laajempien tutkimusten toteuttamisen.