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Injuries to conifer seedlings caused by simulated summer frost and winter desiccation

Lars Christersson & Heinrich A. von Fircks

TIIVISTELMÄ: KESÄHALLOJEN JA TALVISEN KYLMÄKUIVUMISEN AIHEUTTAMAT VAURIOT HAVUPUIDEN TAIMILLA

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Visible frost damage to forest trees in Sweden seldom occurs in winter but is frequent in late spring, summer, and early autumn. Frosts are frequent in all seasons in various parts of Sweden, even in the southernmost part (lat. 56°, N) and temperatures may be as low as –10 °C even around mid-summer. Ice crystal formation within the tissues, which in most seedlings takes place at around –2 °C, causes injury, not the sub-zero temperatures themselves.

The apical meristem, the elongating zone, and the needles of seedlings of *Picea abies* in a growing phase were damaged at about –3 °C and those of *Pinus sylvestris* at about –6 °C. Other species of the genus *Pinus* were tested and most were found to be damaged at about –6 °C, with some variations. *Picea* species tested were damages at about –3 °C to –4 °C.

A method has been designed to compare the response of different species to winter desiccation, which occurs under conditions of (1) low night temperature, (2) very high irradiation and increase in needle temperature during the photoperiod, (3) frozen soil, (4) low wind speed. There were differences in response to winter desiccation between pine and spruce species. Seedlings of *Pinus contorta* tolerated these winter desiccation conditions much better than those of *P. sylvestris* or *Picea abies*. *Picea mariana* was the least tolerant of the species tested.

Pakkasia esiintyy Ruotsissa myös kasvukauden aikana maan kaikissa osissa. Lämpötila voi laskea –10 °C:een myös keskikesällä. Ruotsissa syntyy näkyviä metsäpuiden pakkasvaurioita usein keväällä, kesällä ja syksyllä. Tutkittaessa kuusen (*Picea abies*) taimien kärkikasvusolukon, kasvuvyöhykkeen ja neulasten pakkaskestävyyttä kasvukauden aikana havaittiin vaurioita noin –3 °C lämpötilassa. Mänty (*Pinus sylvestris*) vaurioitui vastaavasti noin –6 °C lämpötilassa. Muut tutkitut *Pinus*-lajit vaurioituivat noin –6 °C, ja *Picea*-lajit noin –3 °C – –4 °C lämpötilassa. Talvisen kylmäkuivumisen vaikutusta taimiin tutkittiin seuravissa olosuhteissa: (1) matala yölämpötila, (2) voimakas säteily valojakson aikana, (3) jäätynyt maa ja (4) alhainen tuulennopeus. *Pinus contorta* kesti näitä olosuhteita huomattavasti paremmin kuin *Pinus sylvestris* tai *Picea abies*. Tutkituista lajeista vähiten kestävä oli *Picea mariana*.

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Authors' address: Department of Forest Ecology, EMC, Swedish University of Agricultural Sciences, Uppsala, Sweden.

1. Introduction

Cold air coming from the Arctic causes occasional frosts during the growing season in Fennoscandia. These so-called advection frosts (Hough 1945, Day and Peace 1946) may cause severe damage to conifer seedlings, particularly spruce (Christersson 1978). Topographic depressions and absence of shelter are conditions associated with summer radiation frost (Day and Peace 1946) during calm and clear nights when the excess of long-wave radiation from the ground causes subzero temperatures. When both advection and radiation frost have occurred simultaneously, temperatures as low as –10 °C in the middle of the growing period on valley bottoms have been recorded in the south of Sweden (Christersson and von Fircks 1984, Christersson et al. 1984).

The reasons why summer frosts occur so often and why summer temperatures drop so low in Fennoscandia are the geographical location, so far to the north, and the direction and the reliability of the Gulf Stream. To explain this we may discuss the situation in detail.

Nowhere in the northern hemisphere do conifer stands extend as far north as in Fennoscandia (perhaps with the exception of stands of *Picea abies* var. obovata in the Khatanga area in Sibiria, long. 103 °E,) (Critchfield and Little 1966, Schmidt-Vogt 1977). In the northern part of Finland and Norway, stands of *Picea abies* are found at latitude 69° N and stands of *Pinus sylvestris* at latitude 70° N. The reason for this is the warm Gulf Stream, originating from and warming up in the Mexican Gulf and along the east coast of North America, then crossing the Atlantic and flowing along the western coast of Great Britain and Norway. The most frequent wind direction in the northern part of Europe is southwesterly, so that the wind has warmed up over the gulf Stream for a long time before it reaches Fennoscandia. Without this warm wind there would be winter conditions in the northern part of Fennoscandia throughout the year, because of cold air coming down from the Arctic, as there are in Greenland and NE Canada, on the other side of the Atlantic Ocean. Of course the risk of a reversal in the climatic conditions for an area influenced by the Gulf Stream increases with latitude.

Clear skies and bright sunshine in combination with relatively low wind speed and low humidity are frequent in late winter and early spring in Fennoscandia. In these conditions, needle temperatures many degrees above zero have been measured (Christersson and Sandstedt 1978, Tranquillini 1979). The death of shoots is associated with frozen soil and frozen stem parts, restricting water transport to the foliage where evaporation is taking place (Equchi et al. 1966, Wardle 1971, Levitt 1980). Sakai (1970) pointed out that desiccation damage is caused by insufficient water supply in conditions of sunshine and low relative humidity. The parts of young conifer seedlings which protrude above the snow cover are often damaged in such conditions, either by desiccation (for a literature review see Tranquillini 1982), photooxidation (Öquist 1983), or most probably by a synergistic effect of both.

We describe the conditions when winter desiccation occurs as (1) clear sky and bright sunshine, (2) air temparature around zero, (3) frozen soil, (4) low wind speed.

The objectives of the present investigation were to study (1) frost hardiness in the growing phase (Christersson 1978) and (2) winter desiccation tolerance of some conifers, particularly genera and species of interest to Nordic silviculture.

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2. Materials and methods

2.1 Plant material

Conifers from different parts of the northern hemisphere (N. America, Fennoscandia) were grown from seeds in containers (35×35×60 mm, Combi cells) in a mixture of sand and peat (50/50) in plastic greenhouses in nurseries in central Sweden (latitude 60–61° N). After the growing season the seedlings set bud outdoors under natural conditions. In November the seedlings were packed in plastic-sealed paper cartons, wrapped in protective plastic and stored at –4°C. For experimets the seedlings were brought out of the cold-store, potted (0.3 dm^3 pot), and transferred to a greenhouse with a photoperiod of 20 hours (daylight plus 200 μE. m^{-2}. s^{-1} from Osram Power stars HQI-E 400 W/Hd), and a temperature of 20°C by day and 15°C at night. After two weeks in the greenhouses the seedlings started to grow and after 4–5 weeks their frost hardiness in the growing phase was determined. The frost desiccation tests were made on seedlings taken directly from the cold store.

2.2 Frost hardiness test

The frost hardiness test was described in detail by Christersson (1978). Shoots of the seedlings were sprayed with water and glass tubes were put over the shoots. Ice crystals were placed into the glass tubes. These procedures were intended to ensure inoculation of ice crystals into the needles of the tested plants with as small a sub-cooling effect as possible.

The pots with the seedlings and the glass tubes were turned upside down and the shoots in the glass tubes were placed into a freezing bath of alcohol. The temperature of the bath was lowered from 0°C to the desired temperatures at a rate of 4°C per hour. The temperature around the roots was about +15°C throughout the tests. After two hours at the pre-determined temperature the shoots were thawed at a rate of 4°C per hour to +4°C. The seedlings were then transferred to greenhouse conditions where they were grown for 7 weeks, after which the Lt $_{50}$ was determined (Christersson 1978). The test was replicated three times.

2.3 Frost desiccation test

Seedlings in the winter phase in containers were thawed overnight at +4°C in darkness and then planted in plastic boxes (12×15×19 cm) with 5 cm of gravel in the bottom and with 12 seedlings in each box. The rooting substrate of the containers was covered with 1 cm of gravel in the box. The plastic boxes were transfered to a walk-in growth chamber and placed in a freezing bath of alcohol at –2°C. The conditions of climate are shown in Fig. 1. At different time intervals, one box of each species was transferred to darkness and +20°C for 12 hours and then to greenhouse conditions.

After 7 weeks the number of seedlings which had budflush was counted. The test was replicated three times.

3. Results

The results of the frost tests of conifer seedlings in the growing phase show differences between both genera and species (Fig. 2). There were no differences between the two tested provenances of *Picea abies*. *Larix decidua* from the north of Sweden tolerated frost during the growing phase to the same extent as provenances of *Larix laricina* from Ontario, Canada. There were no differences between different provenances of *Larix laricina*. Species

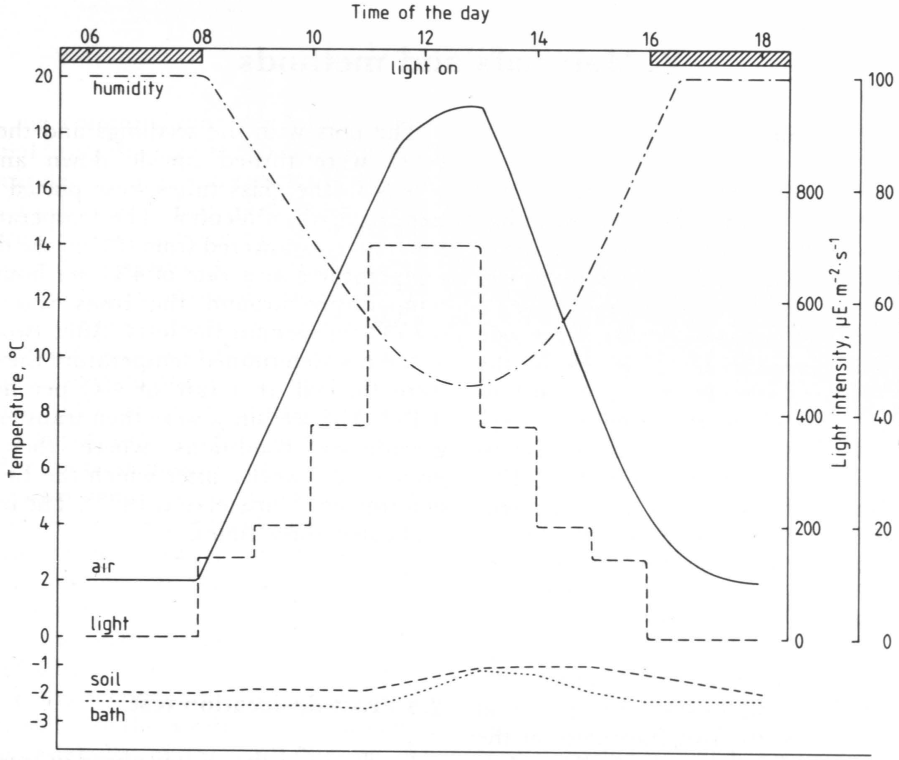

Fig. 1. Climatic conditions in the walk-in growth chamber for the winter desiccation test. The step-wise increase and decrease of light intensity is governed by the switching programme.

of pine were significantly the most frost-hardy in the growing phase, with the exception of *Pinus radiata*. *Pinus contorta* was most frost-hardy. Seedlings of *Pinus sylvestris, P. nigra* and *P. roxburghii* were one degree less hardy while *P. attenuata* and *P. radiata* were the most susceptible species.

The differences between provenances, species and genera were relatively small in this respect. However, in contrast, there were very clear differnces in hardiness among the four tested species in respect to winter desiccation in the winter phase (Fig. 3). LT$_{50}$-values (budflushing) of the seedlings were as follows: *Picea marina* 4 days; *Picea abies* 17 days; *Pinus sylvestris* 27 days, and *Pinus contorta* 43 days.

4. Discussion

The survival of plant seedlings in a regeneration area depends on many environmental factors. The most critical conditions in Sweden are summer frosts and winter desiccation. When analysing the reasons for poor plant survival, it is important to differentiate between the two. The present investigation shows that the correlation between frost hardiness in the growing phase and winter desiccation hardiness during the winter phase may be good, as exemplified by the species *Pinus contorta* ana P. sylvestris (Figs. 2 and 3), or poor, as for species *Picea abies* and *P. mariana* (Figs. 2 and 3).

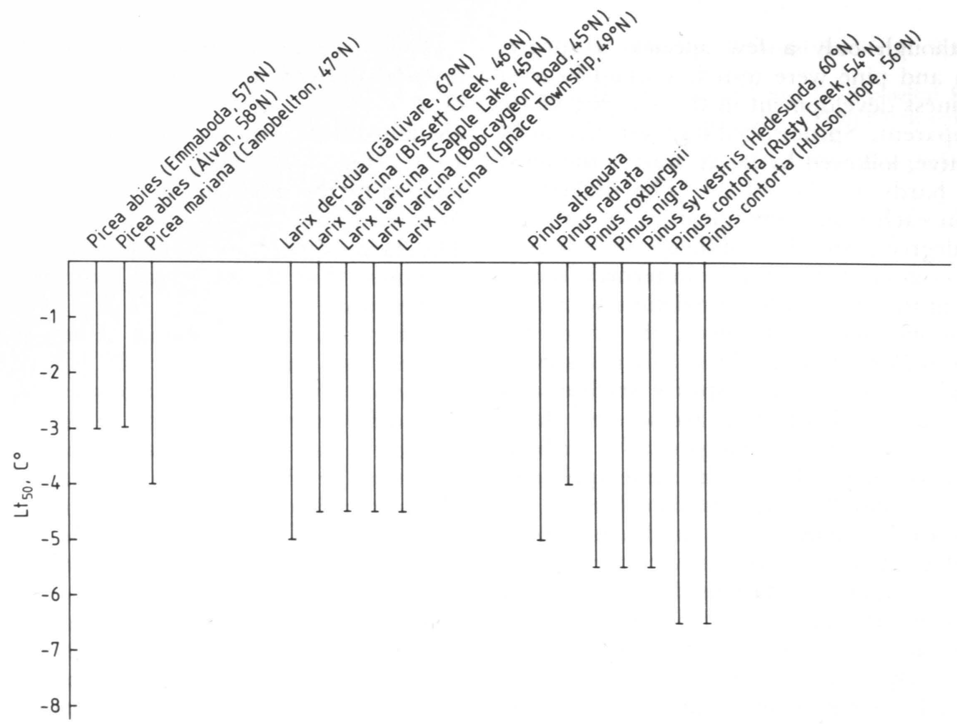

Fig. 2. Lt$_{50}$ of different conifer species in the frost hardiness test. Results are means from three different experiments. Species without a provenance name originated from a French nursery.

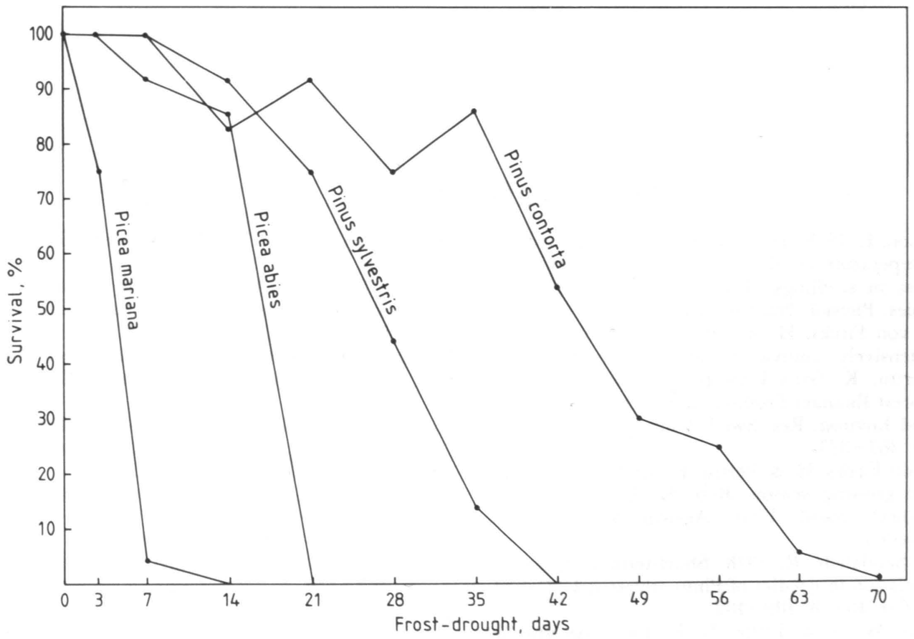

Fig. 3. The percentage survival of seedlings in the winter desiccation test of four conifer species after different numbers of days in the test climate. For details, see the text. The experiments were replicated three times.

Although only a few species of spruce, larch and pine were tested, a trend in frost hardiness development in the growing phase is apparent. Spruce seedlings are the most sensitive, followed by larch. Pine is the most frost hardy in this phase. The differences within each genus amount only to one or a few degrees, and it is difficult to interpret their ecological significance in terms of survival, but this small difference definitely creates an on-off-situator. However, the difference between *Picea abies* and *Pinus sylvestris* is large enough to explain why spruce seedlings in many summer frost areas are severely damaged whereas pine seedlings survive without visible damage. Whether the same applies to *Picea abies* and *P. mariana* is uncertain, as the difference in summer frost hardiness is only one degree. In Swedish silviculture today there are great expectations that seedlings of *P. mariana* will survive and develop in areas that are difficult to reforest (Johansson 1986), particularly in areas close to the mountains. Although the results of the present investigation show better frost hardiness in the growing phase for *Picea mariana,* the winter desiccation hardiness was less than for *P. abies.* More practical tests are needed before planting large areas.

The observations that seedlings of *Pinus contorta* survived much better than seedlings of *P. sylvestris* in frost pockets in Sweden (Stefansson 1957, Remröd 1970, Hagner 1971, Hägglund 1980) can hardly be explained by the difference of one degree in the frost hardiness of the growing phase (Fig. 2). The large difference in winter desiccation hardiness (Fig. 3) is a much more plausible explanation.

Other conifer species will be included in the test, and the present results will be used to develop a viability test for conifer seedlings from different nurseries. The winter desiccation test is particularly suitable. In container nurseries the plant material is stored during winter in plasticsealed paper cartons in a cold store at –4°C. The physiological conditions of plant material of the same species and provenance differ from nursery to nursery. We have indications that seedlings from nurseries that do well in our frost desiccation tests survived harsh conditions much better after being planted on a clear-felled area. More basic research in frost hardiness and desiccation, experimental work, and practical tests in the field are needed before recommendations can be made.

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