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Frost resistance during shoot elongation in Picea abies (L.) Karst. seedlings in relation to the growth environment of the previous growing period

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TIIVISTELMÄ: EDELTÄVÄN KASVUKAUDEN YMPÄRISTÖTEKIJÖIDEN VAIKUTUS KUUSENTAIMIEN PAKKASKESTÄVYYTEEN KASVUVAIHEEN AIKANA

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Frost resistance during shoot elongation in seedlings of Norway spruce was studied in two experiments. The aim of the first study was to evaluate the effect of varying mineral nutrition. Except for potassium, only minor differences in mineral elements concentrations were established, presumably due to low levels of irradiance and thus a low rate of dry matter production. No significant differences in frost injuries were found between the treatments in the experimental series, but the control seedlings were significantly less injured. It is assumed that poor hardiness development at the end of one growth period resulting from low levels of irradiance may decrease the frost resistance during the next shoot elongation phase. Observations from the second experiment with Norway spruce nursery stocks representing different seedling ages and production systems, support this assumption.

Kuusentaimien pakkaskestävyyttä kasvuvaiheen aikana tutkittiin kahdessa kokeessa. Ensimmäisen kokeen tarkoituksena oli tutkia eri ravinteiden pitoisuuksien vaikutusta 1-vuotiaiden taimien pakkaskestävyyteen. Koeryhmien ravinnepitoisuudet eivät poikenneet kaliumia lukuunottamatta merkittävästi toisistaan. Syynä tähän oli ilmeisesti matala säteilytaso ja siitä aiheutunut vähäinen kuiva-ainetuotos. Koeryhmien välillä ei havaittu merkitseviä eroja pakkaskestävyydessä, mutta kontrollitaimien pakkaskestävyys oli merkitsevästi suurempi kuin koetaimien. Tuloksen perusteella asetettiin hypoteesi, jonka mukaan kasvukauden aikana vallitseva matala säteilytaso ja siitä aiheutunut epätäydellinen talveentuminen alentavat seuraavan kasvukauden alussa havaittavaa pakkaskestävyyttä. Toisessa kokeessa tutkittaessa eri ikäisten ja eri tavoin tuotettujen taimien pakkaskestävyyttä saatiin hypoteesiä tukevia tuloksia.

Keywords: Norway spruce, nursery stocks, late-frost resistance, physiological status, hardiness development, irradiance
ODC 181.221.1+174.7 *Picea abies* +181.525+181.2/.3

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1. Introduction

In the Nordic countries late spring frosts are rather frequent (e.g. Andersson 1968, Bjor 1971, Perttu 1981, Bjor and Sandvik 1984). This may often limit successful forest regeneration on clear cut areas. Furthermore, different plant ecotypes differ in susceptibility to late frosts due to variation in time of growth initiation in the spring (e.g. Langlet 1960, Dietrichson 1969).

Larsen (1978) and Dormling (1982) demonstrated that the level of injury after late frosts in conifers may be affected by the physiological status resulting from the growth environment of the previous growing period. It is not yet determined, however, whether the frost resistance could be influenced by the seedling age. Observations from two experiments on these questions in seedlings of Norway spruce (*Picea abies* (L.) Karst.) are reported in this paper.

The first study was designed to evaluate the effect of different mineral nutrient levels on the frost resistance during the second shoot elongation of one-year-old seedlings. The second experiment was a study of frost resistance in the shoot elongation phase in nursery stocks representing different seedling ages and production systems.

This paper is a preliminary report of studies on late frost resistance in Norway spruce. A more comprehensive presentation of the second experiment is being prepared for later publication. I want to thank Oddvar Haveraaen, Martin Sandvik and Øystein Johnsen for valuable comments on the manuscript, Roald Brean and Hans Odde for technical assistance, and Linda Hjeljord and Barbara Thompson for linguistic revision of the text.

2. Materials and methods

2.1 Nutrient status experiment

Norway spruce seeds from southeastern Norway (provenance B2, ≃ 60–61° N, ≃ 8–12° E, 150–250 m asl.) were sown late in June 1985 at Sønsterud forest nursery (60°40' N, 12°4' E). Multipot trays (Hultén 1974) filled with a peat-perlite mixture were used. To prevent growth cessation, the nights were interrupted by light from the end of July.

Early in September, the seedlings were transferred to climate chambers, where the photoperiod and the temperature were changed consecutively in this manner:

- 8 weeks 24/0 h day/night, 20/20° C
- 4 " 18/6 h " , 20/12° C
- 4 " 18/6 h " , 20/8 ° C
- 1 week 16/8 h " , 20/3 ° C

The photon flux density varied between 150–170 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Phillips TL 33), measured with a Li-Cor (LI-185B) photometer. The relative air humidity was kept within 70–80 %.

The basic nutrient solution (Table 1) was composed with a nitrogen content of 7.15 $mmol \cdot l^{-1}$, and with element proportions close to those recommended by Ingestad (1979). There were three experimental series with four levels of potassium (A1–A4), calcium (B1–B4), or concentration of all elements (C1–C4) respectively (Table 2). The pH of the solutions was ajusted to 4.5 by adding sulfuric acid. During the time in the climate chambers, the seedlings were soaked twice weekly by immersing the containers in the nutrient solutions. The solutions were renewed after every fourth use.

After 17 weeks in the climate chambers, the seedlings were stored at 1–2° C for 6 weeks. Upon removal from cold storage, two samples of seven plants each were collected from each treatment for analysis of the needle mineral element concentration. The analysis was performed at the Chemical Research Laboratory, Agricultural University of Norway. The remaining plants were moved into the climate chambers (20/4 h day/night, 22/12°C) to resume growth. As a control group (treatment code D), commercial 1–0 containerized seedlings (provenance B2) were collected from the cold store at Sønsterud nursery and were distributed among the other seedlings in the climate chambers. No nutrients were supplied during the new growth period. The stage of bud flushing (top bud) was recorded according to the scheme of Krutsch (1973). After four weeks the flushing of the leader had reached about stage 6 (shoot elongated, basal needles not yet spread), and the seedlings were freeze-tested.

Table 1. Relative proportions between the mineral elements (nitrogen (7.15 $mmol \cdot l^{-1}$) = 100) in the basic nutrient solution used in the nutrient status experiment.

Element	Relative proportion	Element	Relative proportion
N	100	Fe	0.7
P	16	Mn	0.4
K	50	B	0.2
Ca	5	Cu	0.03
Mg	5	Zn	0.03
S	16	Mo	0.008

Table 2. The concentrations of the varied components in the nutrient solutions (nutrient status experiment). All other concentrations/proportions were kept constant.

Treatment code	Varied component	Concentration	
A1	K	0.13 $mmol \cdot l^{-1}$	
A2		1.28 "	a)
A3		3.84 "	
A4		7.68 "	
B1	Ca	0.04 $mmol \cdot l^{-1}$	
B2		0.12 "	a)
B3		0.38 "	
B4		1.25 "	
C1	Concentration of all elements	50 % of basic solution	
C2		75 % "	
C3		100 % "	a)
C4		125 % "	

a) Equal to the basic nutrient solution.

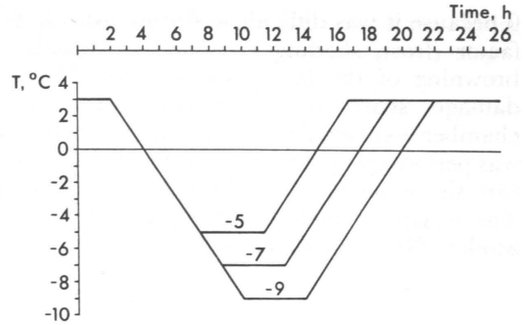

Fig. 1. The freezing programmes at –5, –7, and –9° C in the nutrient status experiment. The cooling and the thawing rate were 1.5 °C·h^{-1}.

The freezing facilities were comprised of four independently cooled chambers, constructed and described by Sjøseth (1971). Consecutive freeze tests at –5, –7, and –9° C were performed (Fig. 1). Twenty seedlings (5 per chamber) from each treatment were frozen at each temperature. Containers of expanded polystyrene and a top cover of perlite protected the roots from freezing. Extensive supercooling was avoided by spraying the needles with cold water (≃ 0° C) when the chamber temperature reached –1° C.

After thawing, the seedlings were kept four hours at 3°C and were then transferred to a greenhouse (20–25° C). The number of frost injured new shoots (laterals and terminals) was counted after three days, and the percent (p) of injured new shoots per plant calculated. The data were transformed to arc sin $\sqrt{p}$ (Snedecor & Cochran 1980, p. 290), before analysis of variance (ANOVA). The treatment means were compared by a Student-Newman-Keuls multiple range test.

Browning and/or discoloration of the previous year needles were recorded after three weeks according to a scale of 0–4 (0 = 0–20 % needles damaged, 4 = 80–100 % needles damaged). Slight injury was included in class

0 because it was difficult to distinguish what factor (frost, shading etc.) had caused the browning of the lowermost needles. Mean damage score (mds) for each freezing chamber was calculated. Analysis of variance was performed on arc sine transformed values (arc sin $\sqrt{(mds/4)}$) (cf. Norell et al. 1986). The treatment means were compared by a Student-Newman-Keuls multiple range test.

2.2 Nursery stock experiment

The plant material was Norway spruce of the same origin as in the nutrient status experiment. Nursery stocks collected from Sønsterud nursery were: One-year-old (1−0) and two-year-old (2−0) containerized seedlings in multipot trays (Hultén 1974), three-year-old (2−1) "KF-plugg" (Froland 1980), and four-year-old (2−2) bare-rooted transplants. The one-year-old seedlings were kept in a greenhouse until removal to the cold store. The other stock types spent their last growth period before lifting outdoors. The 2−2 bare-rooted stock were transferred to cold storage early in October, the other stocks late in October or early in November. These four kinds of stock represented different seedling ages and production systems.

The seedlings were freeze-tested during shoot elongation (approximately stage 7, i.e. shoot elongated, basal needles spread (Krutzsch 1973)) next spring, and the freeze-tests were repeated on similar lots collected from the cold store each spring in 1984, 1985, and 1986. The freezing tests followed the program shown as –5° C on Fig. 1. The methods for evaluation of of frost injuries, calculations, and statistical analysis were identical to those in the first experiment.

3. Results

3.1 Nutrient status experiment

Except for potassium, only minor differences in mineral element concentrations were developed within the experimental series (Table 3). Compared to the optimum range (Ingestad 1962), all levels were supraoptimal. The seedlings of the control group (treatment code D) had element concentrations in the upper part of the optimum range.

There were no significant differences between the treatments in the mean proportions of injured new shoots (Fig. 2). The control seedlings (treatment code D) were significantly less injured at all three testing temperatures. Neither were differences between the experimental treatments found in frost damage on the needles formed the previous growth period (Fig. 3). The control seedlings were also less injured on their first-year needles.

A comparison of the mean stage of bud flushing (top bud) at the time of freezing,

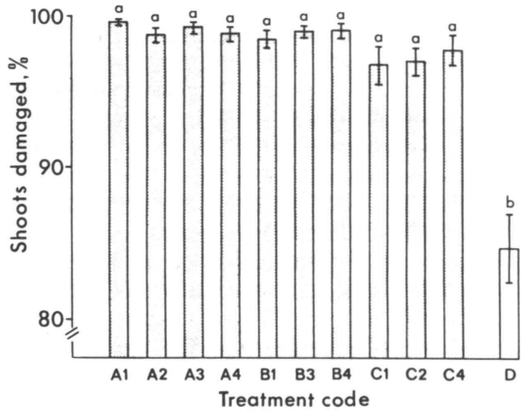

Fig. 2. Mean proportions of new shoots damaged after freeze testing in the nutrient status experiment (pooled results from freeze tests at –5, –7, and –9 °C). Treatments: cf. Table 2, D = control group. The vertical bars show the standard error of means. Treatments with the same letter on top of the histogram are not significantly different (Student−Newman−Keuls multiple range test).

Table 3. Needle mineral element concentrations of the seedlings before growth resumption the year of freeze testing (nutrient status experiment). Mean value of two samples each of seven plants. Optimum range according to Ingestad (1962).

Treatment code	Content, % of needle d.w. N	P	K	Ca	Mg
A1	3.1	0.3	1.6	0.7	0.2
A2, B2, C3	2.9	0.4	1.7	0.7	0.2
A3	2.7	0.3	2.3	0.6	0.2
A4	2.7	0.4	3.1	0.6	0.2
B1	3.0	0.3	1.6	0.6	0.2
B3	2.9	0.4	1.7	0.8	0.2
B4	3.1	0.4	1.7	0.8	0.2
C1	2.7	0.4	1.5	0.7	0.2
C2	2.8	0.4	1.6	0.8	0.2
C4	3.0	0.4	1.8	0.7	0.2
D (control)	2.3	0.3	1.1	0.4	0.2
Optimum range	1.8−2.4	0.1−>0.3	0.7−1.1	0.09−0.6	0.09−0.16

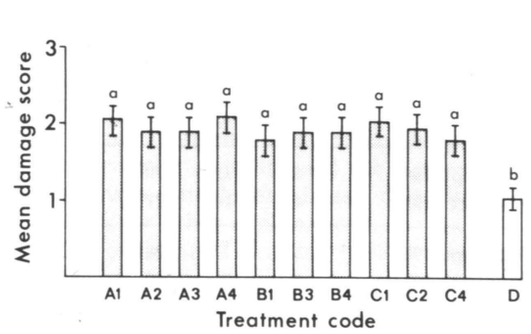

Fig. 3. Mean damage score (0 = 0−20 % needles damaged, 4 = 80−100 % needles damaged) after freeze testing on the first-year needles in the nutrient status experiment (pooled results from freeze tests at –5, –7, and –9 °C). Treatments: cf. Table 2, D = control group. The vertical bars show the standard error of means. Treatments with the same letter on top of the histogram are not significantly different (Student−Newman−Keuls multiple range test).

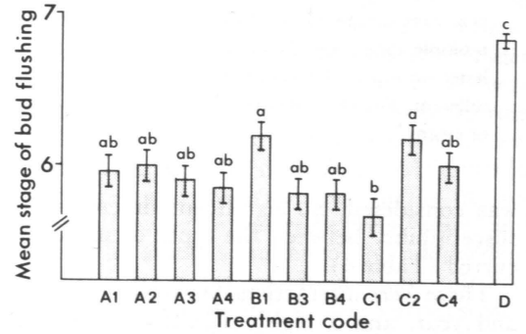

Fig. 4. Mean stage of bud flushing (Krutzsch 1973) at the time of freeze testing in the nutrient status experiment. Treatments: cf. Table 2, D = control group. The vertical bars show the standard error of means. Treatments with the same letter on top of the histogram are not significantly different (Student−Newman−Keuls multiple range test).

showed that the control seedlings flushed earlier than those from the experimental treatments (Fig. 4).

3.2 Nursery stock experiment

One-year-old containerized seedlings of Norway spruce suffered more from freezing at –5° C during shoot elongation in 1984 and 1985 than the other types of stock (Fig. 5). However, when the whole three-year period

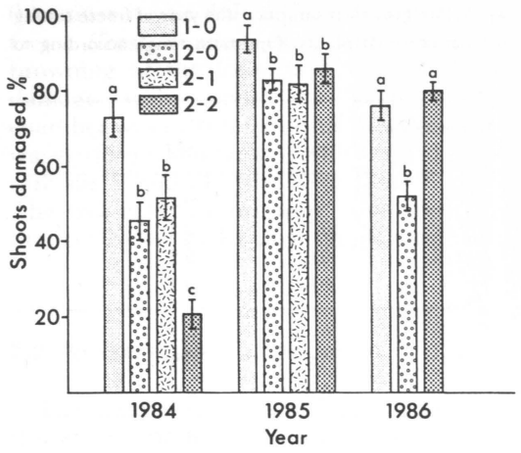

Fig. 5. Mean proportions of new shoots injured after freeze testing of nursery stocks at –5° C in 1984, 1985, and 1986. Nursery stocks: 1–0 = one-year-old containerized seedlings, 2=0 = two-year-old containerized seedlings, 2–1 = three-year-old "KF-plugg" (cf. Froland 1980), 2–2 = four-year-old bare-rooted transplants. The mean values within each year were compared by a Student–Newman–Keuls multiple range test. Nursery stocks with the same letter on top of the histogram are not significantly different. The vertical bars show the standard error of means.

was considered, no significant difference in susceptibility between the types of stock occurred (Table 4).

There were interactions between stock type and year, and a highly significant effect of year on the proportions of injured new shoots (Table 4).

In an attempt to elucidate a possible reason for the significant effect of year on frost damage, data on cloudiness during August-October was compared to the mean level of frost injury (all stocks included) after bud flushing the next spring (Table 5). The new shoots were more susceptible to frost the higher the amount of cloudiness during August-October the previous year. The values of cloudiness were calculated from observations made by Det norske meteorologiske institutt (1983a,b, 1984a,b,c,d, 1985a,b, 1986) at Flisa meteorological station, located about 7 km from the forest nursery. Standard normals (1931–1960) of number of clear and overcast days shows the long time average (Bruun & Håland 1970).

Table 4. Analysis of variance of the factors contributing to the variation in frost injury on newly formed shoots after freeze testing at –5° C. Nursery stock experiment 1984–1986.

Source	SS	df	F
Nursery stock	4.99	3	1.86 ^{ns}
Year	13.12	2	75.50***
Nursery stock × year	4.48	5	10.31***
Error	25.03	288	

Table 5. Observations of cloudiness, in the period August-October in 1983, 1984, and 1985 at Flisa meteorological station, compared to the mean proportion of injured new shoot after freeze testing (–5° C) the next spring. The amount of cloudiness (N) was recorded according to a linear scale of 0–8 three times daily (Det norske meteorologiske institutt 1983a,b, 1984a,b,c,d, 1985a,b, 1986). Symbols: a: mean amount of cloudiness ($\bar{N}$), b: number of clear days (daily sum of $N \leq 4$), c: number of overcast days (daily sum of $N \geq 20$). Standard normals for the period 1931–1960 (Bruun & Håland 1970).

Period	Cloudiness observations a	b	c	Shoots injured %
Aug-Sept 1983	4.6	12	20	
Aug-Oct 1983	4.6	14	27	47
Aug-Sept 1984	5.3	7	28	
Aug-Oct 1984	5.3	11	40	86
Aug-Sept 1985	5.1	6	26	
Aug-Oct 1985	4.9	15	35	70
Aug-Sept (standard	–	3.1	21.7	
Aug-Oct normals)	–	5.6	36.1	

4. Discussion

4.1 Nutrient status experiment

Despite considerable differences in nutrient supply, there were only minor variations in the element concentrations between the treated groups. The analytical results showed supraoptimal levels for all elements considered. This was probably due to the low level of irradiance in the climate chambers. The rate of dry matter production was too low in relation to the rate of nutrient supply (cf. Ingestad 1962, Ingestad & Lund 1986).

The most interesting result was the difference in injury level between the treated groups and the control group. The higher needle mineral element concentration in the experimental series could possibly be an explanation for this. Several authors (e.g. Koskela 1970, Pümpel et al. 1975, Larsen 1978, Aronsson 1980) have reported that increased nitrogen concentrations may act negatively upon resistance to late frosts. This may primarily be a result of the promoting effect of high nitrogen levels on the bud break in spring (Larsen 1978). Since the plants in the treated groups showed the highest nitrogen levels, but flushed latest, there is reason to look for other explanations.

According to Dormling (1982) there is an increasing susceptibility to frost during shoot development until the formation of new terminal buds occurs. In this experiment, however, although the control plants were in the most advanced stage of shoot development at the time of freezing (Fig. 4), they sustained the least damage. It has been demonstrated that wellhardened plants have earlier bud flushing than less hardened ones (Larsen 1978, Sandvik 1978, 1980, Dormling 1982). Despite optimal photoperiod and night temperature, hardiness development is hampered by low levels of irradiance (van den Driessche 1970, Dormling 1972, Sandvik 1978, 1980). Thus, there is reason to believe that the later flushing in the experimental groups was related to poor hardiness development, resulting from the low light intensity in the climate chambers.

On this background, and in agreement with the findings of Larsen (1978) and Dormling (1982), the following hypothesis is proposed: The differences in frost injuries between the treated groups and the control group found in this experiment, may be related to variations in hardiness development at the end of the first growth period, caused by different levels of irradiance.

4.2 Nursery stock experiment

The nursery stocks tested in the second experiment represented four different production systems and thus different growth environments. However, some factor which varied each year and similarly affected all stock types, had the most decisive impact on frost resistance during the shoot elongation phase.

Since the seedlings were pretreated under similar conditions during each year of freeze testing, differences in the environment during the previous growth period should be examined. Among the environmental factors in consideration, the irradiance fulfills the request. This factor varies between years, and affects all stocks simultaneously independent of production system. In a forest nursery, variations in irradiance during a given season are mainly caused by variations in cloudiness. Apparently, there was a relationship between the amount of cloudiness during hardiness development in the autumn, and the mean levels of frost injury the next shoot elongation phase (Table 5). The observations are few, but they support the hypothesis derived from the first experiment.

There is reason to emphasize the preliminarity of these studies. Further experiments are needed to confirm the conclusions. However, the results indicated a possible relationship between irradiance level in the autumn and frost resistance during the shoot elongation next spring in seedlings of Norway spruce. This might be of significance for first-year survival on frost-exposed sites.

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