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Within-population variation in frost damage in Pinus contorta Dougl. seedlings after simulated autumn or late-winter conditions

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(Received 10th May 1985)

Summary

Single-tree progenies from a few populations of *Pinus contorta* were cultivated in a climate chamber and tested with respect to frost tolerance. The plants were exposed to −10° C for three hours during the hardening period, simulating autumn conditions. Single-tree progenies and population samples were exposed to two, six, or twelve large diurnal temperature fluctuations, −10°—+20° C, simulating conditions inducing dehardening during late winter.

Significant differences in frost damage were found between populations as well as between single-tree progenies from one of the populations after freezing during autumn conditions. The family repeatabilities for frost damage exceeded 0.50 in two of the three populations studied.

Damage to plants increased with increasing number of simulated late-winter temperature fluctuations. This was the case both for the roots and the upper parts of the plants. No significant within-population variation in frost damage following exposure to simulated late-winter conditions was obtained. The simulating technique used is laborious and will not be further developed. There was a non-significant, positive relationship between frost damage induced in single-tree progenies by simulated autumn and late-winter conditions.

Key words: *Pinus contorta*, climate chamber, frost damage, within-population variation.

Zusammenfassung

Einzelbaum-Nachkommenschaften einiger Populationen von *Pinus contorta* wurden in einer Klimakammer angezogen und auf ihre Frosttoleranz hin getestet. Die Pflanzen wurden während der Aushärtungsperiode für 3 Stunden einer Temperatur von −10° C ausgesetzt, d. h. es wurden die Bedingungen im Herbst simuliert. Weiterhin wurden Einzelbaum-Nachkommenschaften und solche aus den Populationen 2, 6 oder 12 großen täglichen Temperaturschwankungen von −10° bis +20° C ausgesetzt, um die Bedingungen der Enthärtungsperiode im späten Winter zu induzieren. Sowohl zwischen Populationen als auch zwischen den Einzelbaum-Nachkommenschaften einer der Populationen wurden signifikante Unterschiede bei den Frostschäden gefunden, nachdem die Herbst-Frostbedingungen eingetreten waren. In zwei der drei untersuchten Populationen war der Wiederholbarkeits-Koeffizient für die Frostschäden auf der Familienbasis größer als 0,50. Die Schäden an den Pflanzen nahmen mit zunehmender Anzahl der simulierten Spätwinter-Temperaturschwankungen zu. Dies war der Fall sowohl bei den Wurzeln als auch bei den oberirdischen Pflanzenteilen. Es wurden jedoch keine signifikanten Unterschiede bei den Frostschäden innerhalb der Populationen erzielt, nachdem die Pflanzen den späten Winter-Bedingungen ausgesetzt worden waren. Die angewendete Simuliertechnik ist mühselig und soll nicht weiterentwickelt werden. Es gab eine nicht signifikante, positive Beziehung zwischen den Frostschäden, induziert durch simulierte Herbst- und Spätwinter-Bedingungen.

1 Introduction

For the three conifer species — *Picea abies, Pinus sylvestris, Pinus contorta* — planted in northerly Sweden hardiness is of decisive importance for the success of stand establishment.

In his comprehensive studies of plant survival in *Pinus sylvestris* populations, transferred altitudinally and/or latitudinally, Eiche (1966) unequivocally showed that the plant death originated from injuries occurring during late winter or early spring. He followed the plant death by annual inspection of all the 20 trials distributed over a latitudinal range of 61—68° and related his observations to the

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annual weather conditions at the test sites. Repeated, large temperature fluctuations may be the triggering environmental factor for the lethal frost damage. This was confirmed by Kullman (1983) in his study of a marginal population of *Pinus sylvestris*.

From our studies of *Pinus contorta* and *Pinus sylvestris* in climate chambers we have found that the two species respond to photoperiod and thermoperiod in a similar way with respect to growth cessation and hardening (Ekberg *et al.* 1979). We have also obtained a good correlation between frost damage caused by controlled freezing tests of seedlings cultivated in a climate chamber and the survival in field trials (Jonsson *et al.* 1981). In the above study populations from latitudes 47—63° were tested by freezing at 11—14 h nights following a weekly prolongation of the nights by one hour. In this way we simulated frost exposure during autumn conditions.

The above mentioned correlation with field survival might be due to a correlation between frost tolerance attained during the autumn and the frost tolerance during late winter. Plants hardened late during the season might not attain the same stability against temperature fluctuations during late winter. Another explanation might be that frost tolerance during the autumn and stability against temperature fluctuations during late winter independently of each other are decisive for plant survival.

Since we have studied frost tolerance only in relation to autumn conditions and the critical events under field conditions occur during late winter we found a need for a study of frost tolerance during this period of the year. Other studies of hardiness in *Pinus contorta* have either dealt with growth rhythm or autumn frost tolerance (Rehfeldt 1980; 1983; Rehfeldt and Wykoff 1981). In *Picea sitchensis* Cannell and Sheppard (1982) identified six seasonal phases of frost hardiness. For pines, autumn and late winter are the phases when frost hardiness is most critical for survival in most years.

Recently an extensive breeding program for *Pinus contorta* has been initiated in Sweden. This program ought to be supported by estimates of genetic parameters for important characters. So far no such estimates have been published for *P. contorta.*

One purpose of the present investigation was to develop a technique to simulate conditions inducing frost damage in nature during late winter and to relate the frequency of frost damage induced by use of this technique to damage caused by simulated autumn frosts. The variation of frost tolerance within populations was another subject of the study.

2 Material and Methods

2.1 *Material*

The studies were made on the populations listed in *Table 1.* Frost tolerance attained under *autumn conditions* was studied in populations (stands) Nos. 2, 5 and 6. Six to 12 single-tree progenies from each of these populations were tested, each progeny being represented by 12 plants per test occasion.

Table 1. — The origin of the populations studied.

Population		Latitude (N)	Longitude (W)	Altitude (m)
1) Rusty Creek	Yukon	63°30'	136°30'	760
2) Rusty Creek C	Yukon	63°28'	136°25'	630
3) Carmacks	Yukon	62°08'	135°15'	620
4) Canol Road	Yukon	61°08'	132°38'	1 090
5) Fort Ware	BC	57°20'	125°30'	763
6) Sucker Lake	BC	50°51'	122°49'	970

Populations Nos. 1, 3 and 4 were used in a pilot experiment when developing a feasible technique for investigations of frost tolerance under simulated *late-winter conditions*. The same material was studied in the first experiment dealing with late-winter frost damage, where 12 plants per population and treatment were included. In the second experiment, six single-tree progenies from population No. 5 were studied as regards late-winter frost damage. In this case eight plants per progeny were included in each of the four treatments.

2.2 *Methods*

2.2.1 Autumn frost conditions

We applied the same technique as described previously (Jonsson *et al.* 1981). The principle of this technique is to freeze-test plants at different times following a period of hardening by means of simulating autumn conditions. In this experiment, night lengths were successively prolonged by 1 h per week and the night temperature was lowered from 15° C to 5° C, while the day temperature was 25° C. Freezing tests were performed when a differentiation in frost tolerance within the material was expected to take place; this was estimated on the basis of the results of growth of secondary needles, which is a character correlated with frost tolerance. In the above mentioned experiment, four seedlings per progeny in each of the three blocks were frozen to —10° C during three consecutive nights (one block per night) during the weeks with 11, 12 and 13 h nights, respectively.

2.2.2 Late-winter frost conditions

The principle of the technique used for the investigation of frost damage induced by adverse late-winter conditions is that, after a period of hardening and artificial winter, the seedlings are exposed to large diurnal fluctuations in temperature, which are probably the most important reason for frost damage in late winter.

The experiments can be divided into the following stages: cultivation of the material to obtain a certain plant size, hardening treatment, artificial winter with a gradual drop of the temperature to −10° C, simulating late-winter conditions, successive increase of temperature to temperatures above zero, and exposure of plants to conditions stimulating growth.

Cultivation. After two weeks at 20° C under continuous light, seedlings were potted (pots 8 cm in diameter) in mineral wool and exposed to 20/10° C day/night temperatures and 4 h long nights for eight weeks. A complete nutrient solution 2L 6513 (Ingestad 1979) of low concentration (100 mg N/l and the proportions of N:K:P amounting to 100:65:13) was given 1—2 times a day or 2—3 times a week, depending on the stage of plant development. Relative air humidity was 75 per cent. If not otherwise stated, the light intensity at seedling level was 22 000 lux ($70 W \cdot m^{-2}$, 270—695 nm).

Hardening. The purpose was to start hardening the plants at ten weeks of age by means of light and temperature conditions simulating summer and autumn at a northern locality at high elevation as recorded at Arjeplog, lat. 66°02', alt. 428 m.a.s.l., where demand for frost hardiness is high.

In a pilot experiment, the photo- and thermoperiod were changed after each five-day period, the night being prolonged at the same rate as at Arjeplog, day and night temperatures being based on mean values calculated from meteorological data for summer and autumn months for a

10-year period (1969—1978). The main drawback of this procedure is that extreme temperatures are eliminated from the experiment. We did not find the technique used in the pilot experiment feasible for use in the phytotron.

In the following two experiments a somewhat simplified temperature scheme and weekly changes of light and temperature were used.

Artificial winter. When nights, prolonged successively during the hardening period, had attained 16 h length, the plants were exposed to an artificial winter. Before it started, we checked their expected frost tolerance by means of estimations of dry matter content and elongation of secondary needles (see Jonsson *et al.* 1981). During the artificial winter nights were 16 h long and the temperature was gradually lowered to -10^0 C, over an 8-week period. The control plants, which were not exposed to temperature fluctuations, were kept at this temperature for five weeks.

Simulating late winter conditions. After two weeks of exposure to -10 °C, when the age of the plants was about 30 weeks, treatment simulating late-winter conditions was started. Three treatments were used: 2, 6, and 12 large temperature fluctuations ($-10^0\text{ C} \rightleftarrows +20^0\text{ C}$) performed every other day plus a control material. The change of temperature, brought about by moving freezing trucks between different climate chambers, was stepwise in both directions:

$$-10^0\text{ C} \rightleftarrows -5^0\text{ C} \rightleftarrows +10^0\text{ C} \rightleftarrows +20^0\text{ C}$$

16 h 1/2 h 1 h 5 h

In the chambers with -10^0 C and -5^0 C, only faint bulb light was available. During the first and last hour in the chamber with $+20^0$ C, plants were exposed to 30 000 lux and during the remaining three hours the light intensity was increased to 60 000 lux. The treatment with the largest number of temperature fluctuations was expected to result in the most far-reaching dehardening.

While the upper parts of the plants were exposed to the temperatures described above, the roots were kept at temperatures below zero by means of the freezing trucks.

In the trucks, the outside case contained a box (inside measurements: 37 × 34 × 17 cm) in which 16 pots (8 cm in diameter) with plants were sunk in a layer of sand covered by gravel. In the space under the box a blower was installed with the aid of which the temperature in the substrate around the roots was maintained at -5^0 C while the air temperature in the chamber was -10^0 C. Registration of temperature was carried out both in the air near the apical parts of the plants and near the plant roots, allowing the temperature to be promptly corrected, if necessary. Before the trucks were moved to the chambers with temperatures above zero, for 7 h long exposures of the plants, the space under the box was filled with cooling blocks by means of which the temperature around the roots was maintained below zero.

Exposure to temperatures above zero and classification of frost damage.

After terminating this treatment, all plants were exposed to temperatures increasing gradually to $+20^0$ C, classified according to damage induced by the treatment and finally classified as regards growth ability at 20^0 C and continuous light.

Frost damage was divided into six classes, 0—5 (0 = no visible damage, 5 = dead apical bud), five to seven weeks after treatment had been terminated. At the end of the experiment the roots were divided into three classes, 0—2 (0 = vital, 2 = dead root).

2.2.3 Statistical analyses

Analysis of variance and estimation of variance components:

The linear model used was as follows:

$$y_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + r_k + (\alpha r)_{ik} + p_{ijk} + w_{ijkl}$$

where

y_{ijkl} = an observation of one plant

μ = grand mean

α_i fixed = population effect; $i = 1,2,3$

$\beta_{j(i)} \sim N(0,\sigma^2_\beta)$ = family effect within population; $j = 1,2 \ldots\ldots 12$

$r_k \sim N(0,\sigma^2_r)$ = replication effect; $k = 1,2,3$

$(\alpha r)_{ik} \sim N(0,\sigma^2_{\alpha r})$ = interaction between population and replication

$p_{ijk} \sim N(0,\sigma^2_p)$ = plot effect

$w_{ijkl} \sim N(0,\sigma^2_w)$ = random error within plot = the remainder of the genetic effect between half-sib plants on the same plot and the environmental effect; $l = 1, \ldots\ldots, n_{ijk};\ 1 \leq n_{ijk} \leq 8.$

ANOVA

Source	df	EMS
Population or treatment	$a - 1$	$\sigma^2_e + b\sigma^2_{\alpha r} + c\,\sigma^2_\beta + bc\,\sigma^2_\alpha$
Family within population	$a(b - 1)$	$\sigma^2_e + c\,\sigma^2_\beta$
Replication	$c - 1$	$\sigma^2_e + b\sigma^2_{\alpha r} + ab\,\sigma^2_r$
Population x replication	$(a - 1)(c - 1)$	$\sigma^2_e + b\sigma^2_{\alpha r}$
Plot	$a(b - 1)(c - 1)$	$\sigma^2_e = \sigma^2_w + C\sigma^2_p$
Error within plot	$\sum_{ijk}(n_{ijk} - 1)$	σ^2_w
Total	$\sum_{ijk} n_{ijk} - 1$	

σ^2_α denotes $\dfrac{\sum_1^a(\alpha_i - \bar{\alpha})^2}{a - 1}$

$$C = \left(\frac{1}{abc} \sum_{ijk} \frac{1}{n_{ijk}}\right)^{-1}$$

For the analysis of the simulated late winter frosts, treatment substituted for population in the above model. Moreover, separate analyses were carried out for each population and treatment using the model below:

$$y_{jkl} = \mu + \beta_j + r_k + p_{jk} + w_{jkl}$$

Analysis of variance was performed according to the SAS, PROC GLM and PROC VARCOMP using the fitting constant method to estimate the variance components.

Family repeatability was estimated on an individual tree basis by

$$h^2_{fam} = \frac{\sigma^2_\beta}{\dfrac{\sigma^2_w}{rC} + \dfrac{\sigma^2_p}{r} + \sigma^2_\beta}$$

3 Results and Discussion

3.1 *Frost damage induced by simulated late-winter conditions in populations.*

Differences in frost damage between the three populations (Nos. 1, 3 and 4) studied were small, probably due to the small variation in their latitude of origin (61°08'—63°30' N). This was the reason for pooling the values of the three populations when evaluating the results as to the influence of the number of temperature fluctuations on the extent of frost damage.

As regards damage to the upper part of the plants, the percentage of severely damaged plants increased with an increasing number of temperature fluctuations. Even control plants, which were exposed only to −10° C, were to some extent damaged (see *Figure 1*), which must be attributed to unsatisfactory hardening.

Figure 2 shows the percentage of plants with various degrees of root damage. The results agree with the results for the upper part of the plants - even the control plants were damaged to some degree and the extent of the damage increased with the number of temperature fluctuations. Thus, even roots were negatively influenced by the temperature fluctuations. It was not possible, however, to determine if the root damage was primary or a consequence of the damage to the upper part of the plants.

3.2 *Variation in frost hardiness within populations.*

3.2.1 Autumn conditions

The results from the freezing test at 12 h nights are illustrated in *Figure 3*. The results from the ANOVAS are presented in *Table 2*. Within-population variation was studied on three populations from the latitudinal range of 50—63°. This means that the mean frost damage score of the populations was expected to vary considerably (cf Jons-

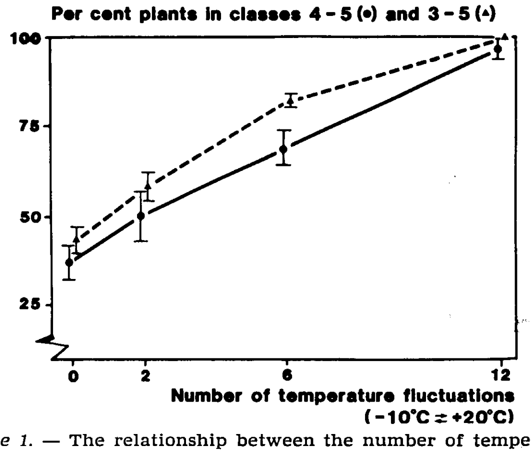
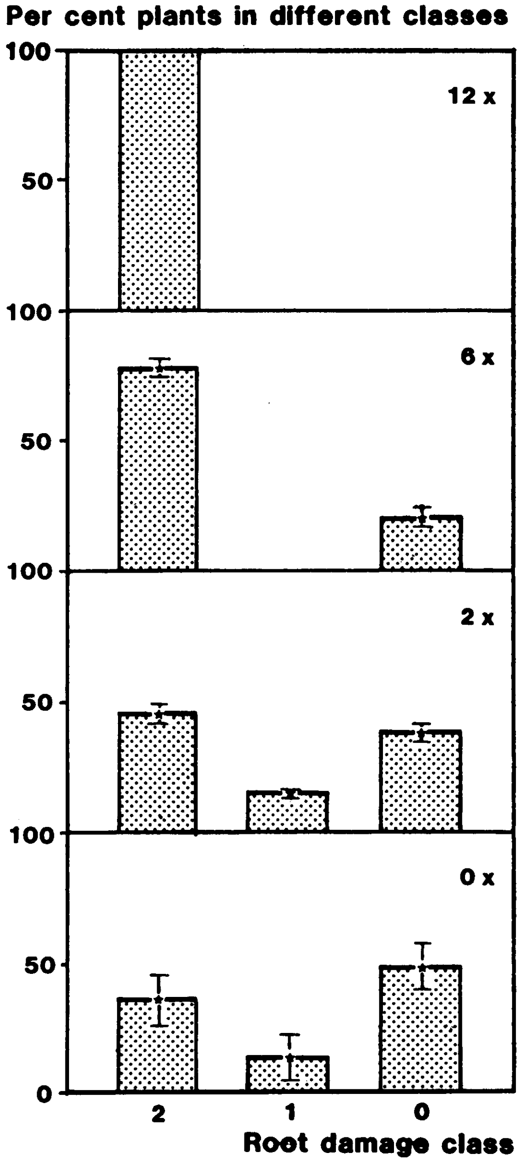


Figure 1. — The relationship between the number of temperature fluctuations between −10° C and + 20° C and the extent of damage. Frost damage was divided into classes 0—5 (0 = no visible damage, 5 = dead apical bud) seven weeks after termination of the treatment. Vertical bars denote ± one standard error based on the population mean values.



0 = vital root
1 = root with low vitality
2 = dead root
Vertical bars denote ± one standard error.

Figure 2. — Percentage of plants with various degrees of root damage after treatment with 12, 6, 2 and 0 temperature fluctuations. Root damage was classified seven weeks after termination of the treatment.

Table 2. — ANOVA of mean frost damage score after freezing at a night length of 12 h during the hardening calculated for individual populations.

	Rusty Creek C				Fort Ware				Sucker Lake			
Source	Df	Mean square	F-ratios	Variance component	Df	Mean square	F-ratios	Variance component	Df	Mean square	F-ratios	Variance component
Family	11	1.47	2.06	0.063	11	3.71	3.28**	0.216	5	0.122	1.38	0.003
Replication	2	7.56	10.61***	0.142	2	8.91	6.17**	0.164	2	0.056	0.43	-0.001
Plot	22	0.715	1.00	0.000	22	1.13	0.78	-0.080	10	0.088	0.69	-0.010
Error within plot	107	0.713		0.713	107	1.44		1.44	54	0.130		0.129
Family repeatability				0.51				0.64				0.20

Table 3. — ANOVA of mean frost damage score after treatment with simulated late - winter conditions calculated for six open pollinated progenies in population Fort Ware.

Source	Df	Mean square	F-ratio	Variance component
Treatment	3	10.06	6.74**	0.165
Family	20	1.55	1.96*	0.097
Replication	2	1.05	0.78	-0.005
Treatment x block	6	1.35	1.86	0.037
Plot	40	0.76	1.06	0.016
Error within plot	120	0.72		0.722
Family repeatability				0.49

son *et al.* 1981; Lindgren 1983). A significant difference between the populations was noted (see also *Figure 3).* This makes a comparison of the genetic variation in frost tolerance within each of the three populations impossible in the same freezing test. With low and high population means of frost damage score the within-population variation will be lower than at intermediate frost damage scores. The results from the separate ANOVAS for each of the three populations are shown in *Table 2.* We obtained significant between-family variation only for population Fort Ware. The southerly population was so close to lethal damage that only limited variation was noted.

In the northerly population, Rusty Creek, which was tested also at 11 h night, the average level of damage was low with small possibilities of revealing any within-population variation. Conversely the results from freezing tests of the southerly population, Sucker Lake, at 13 h night still had such a high average level of damage that no within-population variation could be proven in this case either. In the Fort Ware population the within-population variation after the freezing test at 13 h nights was significant ($p < 0.01$). The correlation between the family mean frost damage in Fort Ware after freezing at 12 and 13 h nights respectively was high, $r = 0.77^{**}$, showing that ranking of the progenies within this population was fairly consistent.

From *Table 2* it is seen that rather high family repeatabilites for populations Rusty Creek C and Fort Ware were obtained. The repeatabilities would probably rise if the freezing test could be carried out at such a night length that the population mean frost damage score would be close to 2.5. The results obtained indicate that family selection for frost tolerance would be possible in *Pinus contorta* breeding.

The large within-population variation noted for *P. contorta* agrees well with results from other northern temperate pines (Wright 1963; Dietrichson 1970; Eriksson *et al.* 1976; Perry and Lotan 1978; Mikola 1982; Stahl 1984; Norell *et al.* 1986).

The differences between blocks were significant in some cases. This might partly be attributed to the methods used, since the date of freezing varied by 1—2 days between blocks. As hardening is a continuous process, frost tolerance increased during this time. This was proven by Norell *et al.* (1985) in a similar study with *Pinus sylvestris.*

3.2.2 Late-winter conditions

Owing to the limited space available we could only study the within-population variation in one population, No. 5, Fort. Ware. The results obtained *(Table 3* and *Figure 4)* showed a strongly significant effect of the treatments but also a weakly significant effect on the family level. When a separate ANOVA was run for each treatment, the between-progeny variation was found to be nonsignificant for all treatments.

The technique used by us to simulate late-winter conditions is laborious and space demanding. It is possible that good estimates of late-winter frost tolerance could be obtained by means of the technique used by Larsen (1978), who studied the drought resistance in *Pseudotsuga menziesii* provenances.

3.3 *The relationship between damage induced under autumn and late-winter conditions*

Six progenies from the Fort Ware stand were selected to study the relationship between the degree of damage induced by adverse autumn and late-winter conditions, re-

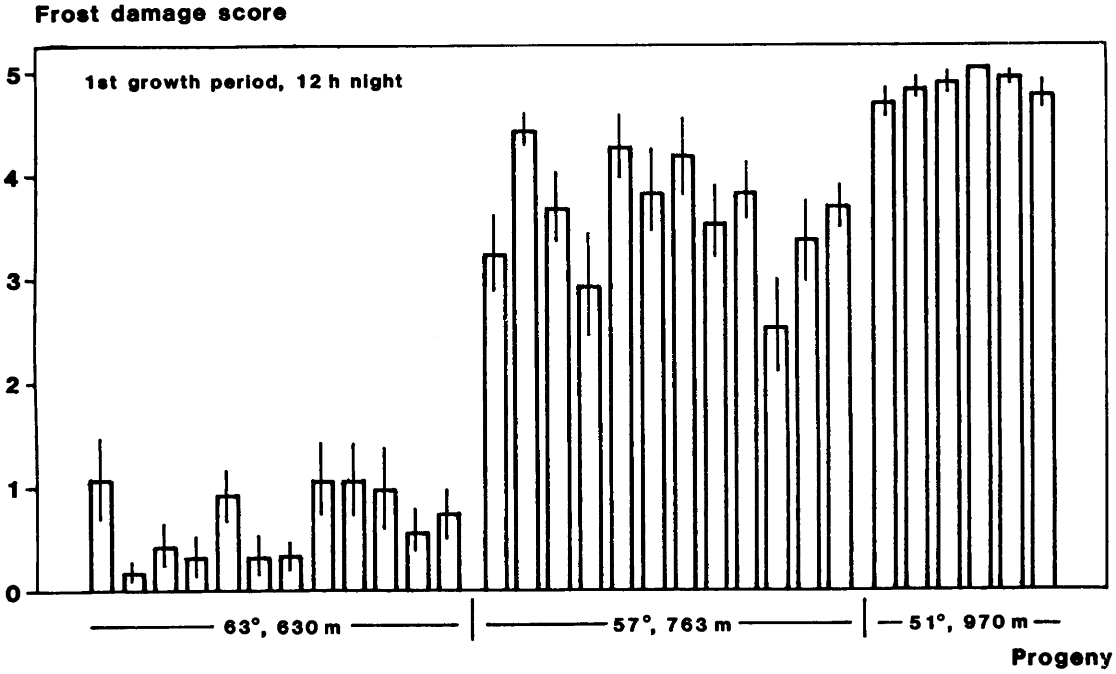


Figure 3. — Mean frost damage score induced by autumn freezing to −10° C at 12h nights in 30 single-tree progenies from three stands. Frost damage was divided into classes 0—5 (0 = no visible damage, 5 = dead apical bud) two weeks after the freezing test. Vertical bars denote ± one standard error.

spectively. The reason for the choice of Fort Ware was that the within-population variation of damage induced during the previously performed autumn freezing test was largest within this stand.

To get values based on as many plants as possible (n = 32), the following evaluation of results from the experiment concerning late-winter conditions was carried out: The ratio between the frost damage score of a progeny and the mean frost damage score of the six families within a treatment was calculated and referred to as relative values. After calculating such relative values for each progeny within each of the four treatments, the mean of these four relative values was calculated for each progeny. Several correlations were calculated between those values and the values of damage obtained in the experiment with autumn freezing tests performed at different night lengths. A positive relationship between the degree of damage induced during autumn and late-winter conditions was revealed in all cases, but none of the correlation coefficients were significant. The strongest relationship between late-winter and autumn damage is shown in *Figure 5*. With the limited within-population variation after late-winter frost simulations, only weak correlations were expected. The data obtained do not make it possible to disclose if autumn and late-winter frost damage are correlated or independent phenomena.

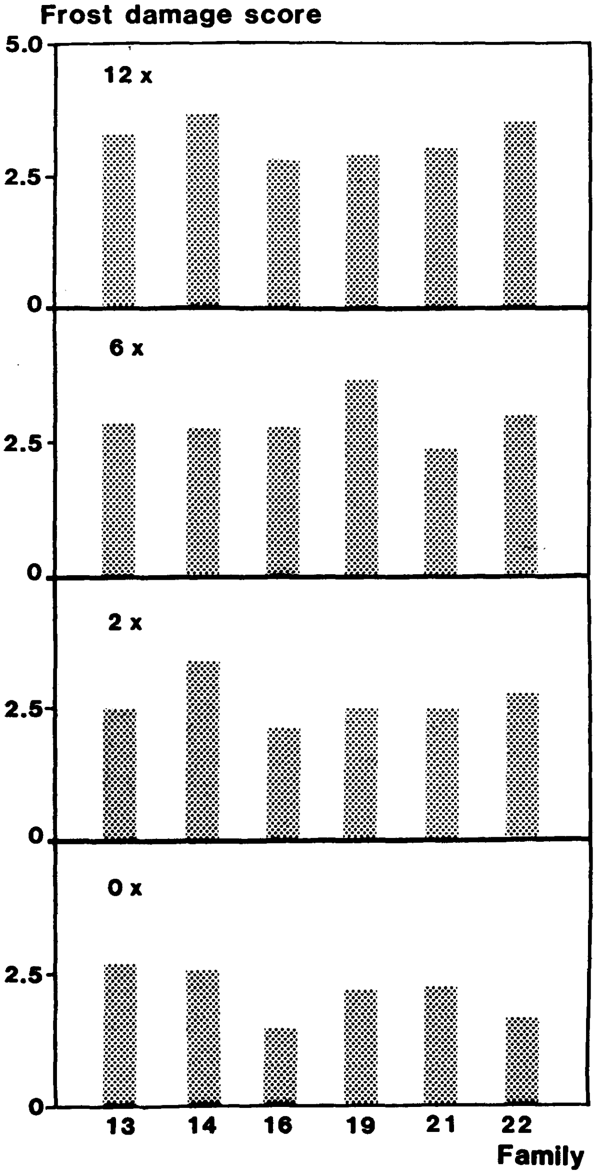


Figure 4. — Mean frost damage score induced in six families from Fort Ware by treatment with 12, 6, 2 and 0 temperature fluctuations simulating late-winter conditions. Division into classes 0—5 (see *Figure 1*) five weeks after termination of the treatment.

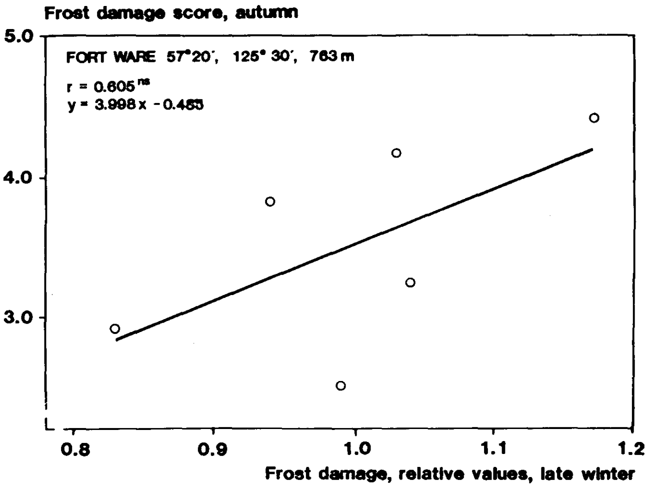


Figure 5. — Regression of mean frost damage score induced under autumn conditions (first growth period, 12 h nights) on relative frost damage (explained in section 3.3) induced under late-winter conditions.

4 Conclusions

The damage to plants increased with an increasing number of temperature fluctuations simulating late-winter conditions. The technique used in simulating late-winter frost conditions is a laborious and space demanding one. We do not intend to develop it further.

There was a great within-population variation in frost damage induced by simulated autumn frosts when the population as a whole was neither too severely nor too slightly damaged (population mean frost damage score was close to 2.5). Moderately high family repeatabilities were obtained for some of the populations, which means that family selection for autumn frost tolerance might be advantageous.

Within the same material there was a positive relationship between autumn and late-winter frost tolerance but the correlation coefficients were not significant.

5 Acknowledgement

We are very grateful to Ingegerd Dormling and Inger Ekberg for detailed discussions of this project and to Dag Lindgren for reading and commenting of the manuscript. We also wish to express our sincere thanks to the staff of the phytotron in Stockholm and at our department in Uppsala for cultivation of the plant material and other skilful technical assistance. The investigation was supported by a grant from the Swedish Council for Forestry and Agricultural Research.

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Estimates of Outcrossing Rates in Six Populations of Black Spruce in Central New Brunswick

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(Received 2nd July 1985)

Abstract

Single-locus outcrossing rates in six populations of black spruce *(Picea mariana* [Mill.] B. S. P.) were estimated based on allozyme data from six polymorphic loci using maximum likelihood methods. Multi-locus estimates were also calculated.

An average single-locus estimate of 0.932 was obtained for the outcrossing rate compared with a multi-locus average of 0.924. There was little evidence of a downward bias in single-locus estimates resulting from non-random forms of mating other than selfing, indicating a lack of development of family clustering.

In four of the populations the observed inbreeding coefficient was negative and significantly less than the expected equilibrium inbreeding coefficient. Gametic and post-zygotic selection favouring heterozygotes is proposed as an explanation. In one population the observed inbreeding coefficient was greater than that expected under equilibrium, possibly suggesting an inbred maternal population.

Key words: *Picea mariana*, isozymes, mating system, heterozygosity, inbreeding.

Zusammenfassung

Fremdbefruchtungsraten wurden durch Untersuchungen einzelner Loci in 6 Populationen von *Picea mariana* ermittelt, wobei 6 polymorphe Loci und die Methode der größten Wahrscheinlichkeiten verwendet wurden. Schätzungen, die auf mehreren Loci beruhten, wurden ebenfalls durchgeführt.

Die durchschnittliche Fremdbefruchtungsrate betrug 0.932 auf der Basis einzelner Loci und 0.924 auf der Basis mehrerer. Es gab wenig Anzeichen für eine Verringerung der Einzel-Locus Schätzung durch Abweichung von zufälliger Paarung außer Selbstbefruchtung, sodaß eine Familienstruktur der Bestände kaum anzunehmen ist.

In 4 Populationen war der Inzuchtkoeffizient negativ und signifikant geringer als der erwartete Gleichgewichtswert. Es wird vorgeschlagen, daß die Erklärung in gametischer und post-zygotischer Auslese zu suchen ist, wobei die Heterozygoten bevorteilt werden. In einer Population war der Inzuchtkoeffizient größer als der erwartete Gleichgewichtswert, was womöglich auf Inzucht in der mütterlichen Population zurückzuführen ist.

Introduction

The pattern by which gametes are united to pass genes from one generation to the next is termed the mating system (Stern and Roche 1974). In the past, species were often characterised as "inbreeders" or "outbreeders", "self-fertile" or "self-sterile". However, it is now recognised that the mating system is far from being a fixed, species-specific constant, but is rather a dynamic entity, varying in time and space and affected by a large number of biotic and abiotic factors. These include the degree of selfcompatability, population density, variation in phenology and climatic variables (Stern and Roche 1974).

The mating system of a species affects the genetic structure of populations - the distribution of genotypes and the dynamics of this structure in relation to evolutionary forces (Jain 1975, Brown 1978, Ritland and Jain 1981). In addition, the estimation of many genetic parameters on which breeding strategies are based makes use of an assumption of random mating which may not be valid (Squillace 1974).

Most models used in describing the mating system consider the production of progeny from an outcross event with probability t to a pollen pool with allele frequency p. Since both of these parameters are unknown, they must be estimated simultaneously (Ritland and Jain 1981). The estimates of t obtained by the observation of progeny genotypes will be affected by other forms of non-random mating

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