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Influence of the female flowering environment on autumn frost-hardiness of *Picea abies* progenies

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Abstract Two experiments were designed to test possible effects of photoperiod and temperature during microsporogensis to anthesis on early autumn frost-hardiness of *Picea abies* progenies. Pollen lots were produced in phytotron rooms and used in crosses in a seed orchard. No biologically important differences in progeny performance were evident either between high and low temperature or between long- and short-day treatments, and no significant interaction between photoperiod and temperature was found. In a third experiment, however, an effect of the environment during female flowering was obtained. Crosses performed in early spring (March) inside a heated greenhouse (short day, high temperature) produced progenies which were less hardy than their full-sibs reproduced from crosses indoors (long day, high temperature) and outdoors (long day, low temperature) in May. The most hardy siblings originated from the late-spring outdoor crosses. These results indicate that some stages in reproduction during female flowering, such as female meiosis, pollen tube growth, syngamy, early embryogenesis and embryo competition, may be sensitive to temperature and/or photoperiodic signals which can be transmitted to the progeny. We suspect that the altered performance of the progenies could be due to an activation of a regulatory mechanism affecting the expression of genes controlling adaptive traits. Both the present and earlier results have implications for the genetic interpretation of provenance differences in Norway spruce.

Key words Pre-conditioning · After-effects · Microsporogenesis · Pollen selection · Embryogenesis · Imprinting · Gene regulation · Provenance variation · Photoperiod · Temperature

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Introduction

An important strategy for breeding and seed production in boreal conifer trees has been to locate seed orchards and clone banks in warm regions. A more frequent, abundant flowering and better seed ripening under favourable climatic conditions are the main reasons for this practice. This strategy has been chosen in Norway too, and several seed orchards have been established during the last 30 years. In some of these orchards, the vegetatively propagated clones have been moved long distances from north to south or from high to low elevation.

Recent results with Norway spruce [*Picea abies* (L.) Karst.] in particular, but also with Scots pine [*Pinus sylvestris* (L.)], have however shown that both climate and weather during sexual reproduction may influence the adaptive properties of the progeny (Bjørnstad 1981; Johnsen 1988, 1989 a, b; Johnsen et al. 1989; Dormling and Johnsen 1992; Andersson 1994; Johnsen and Østreng 1994; Skrøppa et al. 1994; Lindgren and Wei 1994; Skrøppa 1994; Kohmann and Johnsen 1994). The seeds produced under warm conditions give rise to seedlings with later flushing, an extended growth period and a delayed development of frost hardiness during early autumn compared with seedlings from seeds of the same parents reproduced under colder conditions. Even a short forcing period at an elevated temperature in a greenhouse during pollination and early embryogenesis seems to be sufficient to induce reduced autumn frost-hardiness of the progeny (Johnsen et al. 1995). The effects of the parental environment are long-lasting; data indicate that they can endure for at least 17 years from seed (Edvardsen 1995).

So far, it has neither been proven that the observed effects are due to genetic factors nor that they are inherited.

During reproduction, however, there are several processes that potentially may cause genetic or epigenetic changes which could be expressed in the progeny (Skrøppa and Johnsen 1994). Generally, knowledge and consequences of events such as meiotic drive, selection during pollen development, and embryo competition, are lacking for forest trees, even though segregation distortion for paternal gametes and differences in paternal success between pollen parents have been observed (Owens and Blake 1985; Cheliak et al. 1987; Skrøppa and Lindgren 1994). Genomic imprinting is being increasingly accepted as a fundamental and widespread process that determines, in ways not predicted by the laws of Mendelian inheritance, whether a particular gene will be expressed or not (Matzke and Matzke 1993). Such gene regulation, caused by activation or de-activation of certain genes by environmental conditions during reproduction, could affect phenotypic expression (Meyer et al. 1992), but so far no such information is available for forest trees. Moreover, we do not know for sure the kind of environmental triggers which might be involved, even if the most likely candidates are temperature and/or photoperiod (Kohmann and Johnsen 1994; Skrøppa 1994; Skrøppa et al. 1994; Johnsen et al. 1995).

Before any molecular characterization of the causal mechanism(s) can be attempted, the stage(s) of the reproductive cycle which is (are) able to transduce environmental signals from parents to offspring must be identified. We report and discuss data from three experiments. In two of them we test the hypothesis that some changes occur during male meiosis and pollen maturation (before pollination) as a result of differences in photoperiod and temperature given during pollen development. The third experiment tests the hypothesis that changes occur at some stages during female flowering including female meiosis, pollination, pollen-tube growth, syngamy, and early embryo development, in response to treatments given to the female parents inside and outside a heated greenhouse. In all experiments the progenies were tested for the presence or absence of differences in autumn frost-hardiness in relation to the treatments given to the parents during sexual reproduction.

Materials and methods

Origin of the parents

Eight mother clones originating from southeastern Norway (60–62°N, 350–600 m asl), and four father clones from southern Sweden (57–58°N, 200–300 m asl) were used in experiment 1. The parents in experiment 2 comprised four female clones, two from Dolina, Ukraine (49°N, 500 m asl), and two from Mari-dalen, Norway (60°N, 230 m asl), and five male clones, two originating from northern Norway (66°N, 80 m asl) and three originating from southern Sweden (57–58°N, 190–310 m asl). In experiment 3, six mother clones from the south-eastern part of Norway (60°30′–61°30′N, 170–340 m asl) and six father clones were used. Two fathers originated from south-eastern Norway (60°30′–61°30′N, 170–250 m asl), and four fathers were from Sweden (57–58°N, 200–300 m asl).

Pollen treatments

In all experiments male flowering was induced by using long heat treatment as described by Johnsen et al. (1994). Experiment 1 was designed to test the possible effects of temperature and photoperiodic treatments during male meiosis and pollen production on the progeny performance. On March 11 (1992) the grafts of four clones were moved into the phytotron at the University of Oslo. The male clones were given four treatments; long day/high temperature (LD/HT), long day/low temperature (LD/LT), short day/high temperature (SD/HT), and short day/low temperature (SD/LT). The treatments are shown in Table 1. The light intensity was 200 μmol $m^{-2} s^{-1}$ and relative humidity was set to 70% during pollen-cone development. However, when the cones were mature and ready to release pollen, the grafts were moved to dry conditions (less than 30% relative humidity) at 22°C, and pollen was collected directly from the branches. Most of the pollen was released within 3–5 days under dry conditions. Pollen was cleaned and dried at room temperature, and approximately 7–8-ml samples of pollen were then placed in 15-ml vials and sealed.

Experiment 2 was designed to test the possible effects of temperature treatments during male meiosis and pollen production on the progeny performance. Grafts with dormant male-cone buds were moved into the phytotron at the University of Tromsø and the University of Oslo in 1993. In both phytotrons each clone was given a high and a low temperature treatment during meiosis and pollen maturation (Table 2). The light intensity varied in Tromsø due to the use of daylight phytotron rooms and artificial supplementary lighting (Philips fluorescence tubes TLD 84) which gave 150 μmol $m^{-2} s^{-1}$ at night. The light intensity in the phytotron rooms in Oslo was 200 μmol $m^{-2} s^{-1}$. Humidity was set to 70% during pollen-cone development. Three days before pollen shed the grafts were moved to dry conditions and pollen was extracted as described in experiment 1.

Table 1 Treatments (day length/temperature) given to the males during meiosis and pollen maturation. LD = long day, SD = short day, HT = high temperature and LT = low temperature

Treatments		Weeks					
		1	2	3	4	5	6
LD/HT	°C, day/night	12/9	13/10	14/11	15/12	–	–
	Day length (h)	16	17	18	19	–	–
LD/LT	°C, day/night	9/5	10/6	11/7	12/8	13/9	14/10
	Day length (h)	16	17	18	19	20	21
SD/HT	°C, day/night	12/9	13/10	14/11	15/12	16/13	–
	Day length (h)	12	12.5	13	13.5	14	–
SD/LT	°C, day/night	9/5	10/6	11/7	12/8	13/9	14/10
	Day length (h)	12	12.5	13	13.5	14	14.5

Table 2 Temperature treatment (day/night °C) during pollen maturation in Tromsø and Oslo. LT = low temperature treatment, HT = high temperature treatment

Location		Week									
		9	10	11	12	13	14	15	16	17	18
Tromsø	LT	7/5	8/5	9/5	10/5	11/5	12/6	13/7			
	HT	12/10	13/11	14/12	15/13	16/14	–	–			
Oslo	LT						5/5	7/7	9/9	14/14	14/14
	HT						10/10	12/12	14/14	18/18	–

Experiment 3 was designed to test the possible effects on the progeny of heat and photoperiodic treatment given to the female clones. Thus, no treatment differences during pollen development were introduced in experiment 3. Grafts with dormant male-cone buds were moved into a heated greenhouse on February 4, 1993. For the first 5 days they were given temperatures slightly above 0°C. The temperature was increased to 9/5°C (day/night) for the next 2 weeks, then 11/7°C for 1 week, 12/8°C for the next week, then 13/9°C for 1 week and finally 15/11 for 1 week. Pollen was forced at 20–22°C, while day and night and humidity was reduced by using extensive heat and open ventilation in the greenhouse. Pollen was extracted over the period March 22–25.

Crosses performed

In experiment 1 and 2, female flowering occurred naturally on clones in two seed orchards. In experiment 3, female flowering was induced by using stem injections of 2 mg of $GA_{4/7}$ (dissolved in 0.5 ml ethanol) in combination with a short heat treatment (elevated heat from 90% of shoot elongation; Johnsen et al. 1994).

The female flower buds were bagged prior to opening in all three experiments. In experiment 1, crosses were performed in the spring of 1992 at Drogseth seed orchard (61°N, 400 m asl). Pollen from each of four male clones was employed to pollinate two female clones, using four adjacent grafts of the same mother clone per male and pollen treatment (one graft per pollen treatment per cross). Pollination took place four times during the period May 22–25.

In experiment 2, the crosses were performed over the period May 6–12 in an experimental seed orchard at Hoxmark, Ås (59°40′N, 90 m asl). These clones had been planted in the orchard in a randomized design with plots of two ramets (grafts) of each clone standing adjacent to each other. One graft received pollen from a HT treatment and the other graft received LT-pollen.

In experiment 3, identical single-pair crosses (unrelated parents) were performed in three crossing environments in the spring of 1994 at Biri nursery (61°N, 150 m asl): an early crossing indoors (using a heated greenhouse), a late crossing indoors and a late crossing outdoors. Temperature and the accumulated heat sum during the different treatment periods, time of pollination, and days when 450 day-degrees (threshold temperature=5°C; Sarvas 1968) were reached in each treatment are shown in Fig. 1. The mother grafts for the early crosses indoors were moved into the greenhouse on March 8. The temperatures were set to 12/8°C (day/night) and then increased gradually (Fig. 1). Pollination took place from March 27 to April 2 at temperatures from 16–20°C. The late crosses inside the greenhouse started in early May. Female grafts were moved into the greenhouse on May 5. Pollination took place from May 10 to 15. The pollinations outside the greenhouse were initiated on May 10 and were terminated on May 18. All the female grafts that had been treated inside the greenhouse were moved out on June 11.

Cultivation of plants and freezing tests

In all experiments the seedlings were grown and hardened in the phytotron at The University of Oslo and freeze tested as described previously (Johnsen 1989 c; Johnsen et al. 1995). Plants were harvested for freezing tests when the night reached 13 or 14 h. The freezing test temperatures were –8, –9, –10, –11, –12, and –13°C at 12 and 13 h per night in experiment 1, –9, –10, –11, –12, –13, and –14°C at 13 h per night in experiment 2, and finally –11, –12, –13, –14, –15 and –16°C at 14 h per night in experiment 3. Three weeks after freezing, frost damage on needles (browning and discoloration) was scored based on a scale from 0 to 11 where: 0=no visible damage; 1–10=10% increments of brown or discolored needles; and 11=all needles completely brown (Johnsen 1989 c).

Experimental design and statistical analyses

During growth and cold acclimation, plants were grown in phytotron rooms with 4–10 replicates within rooms depending on the experiment. The design was split plots with seedlings of one family and all parental treatments within the family growing adjacent to each other in all three experiments. Plants were harvested, sorted and placed

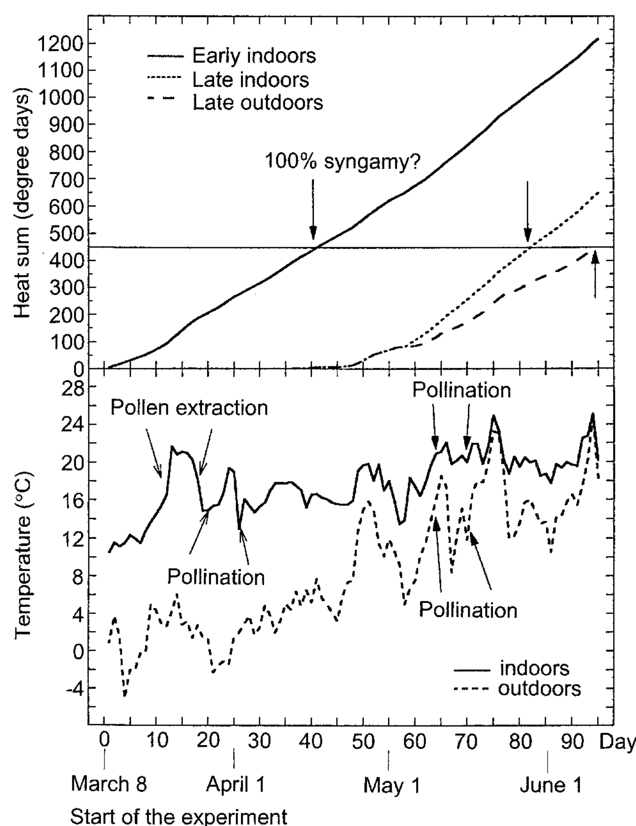

Fig. 1 The mean daily temperatures inside and outside the greenhouse from the start of experiment 3 during the spring of 1993 (lower part). Accumulated heat (threshold temperature of 5°C) in degree days during female flowering in the three treatments (upper part). The *arrows* indicate, according to Sarvas (1968), when approximately 100% of the syngamic events should have occurred in the three treatments

in new containers at the start of the freezing tests. In each freezing chamber, each family and the parental treatment within that family was replicated corresponding to the number of replicates within the room. The seedlings from different parental treatments within a family that had grown adjacent to each other in the phytotron rooms were grouped and also placed adjacent to each other in the freezing chambers. In all experiment, each combination of family and treatment comprised 20 plants per test temperature.

The analyses of variance of frost damage were performed with the GLM procedure (SAS Institute Inc. 1989) by the use of an arcsin transformation of the damage-assessment score as described previously (Johnsen 1989 c; Johnsen et al. 1995). The plot means of two plants were used as the observation unit in experiment 1 and 3, and a plot mean of five plants was used in experiment 2. In all the experiments, the family and replicate were regarded as random and the parental treatment and freezing temperature as fixed effects. The interaction between parental treatment and family was used as the error term in statistical tests of significant treatment effects.

Results

In experiment 1, no effects of photoperiod and temperature on male meiosis and pollen development (Fig. 2), and no significant interaction between pollen photoperiod and temperature, were evident (P=0.20). The result of experiment 2 confirmed what was found in experiment 1 (Fig. 3). No significant effect of pollen temperature was present and this was consistent in all the families included.

The crossing environment significantly affected the hardiness of the progeny in experiment 3 (Fig. 4; Table 3). The progenies from the early indoor crosses were more damaged than progenies from the late indoor crosses (P<0.0001; over all families), which in turn were significantly more damaged than progenies from the late crosses performed outdoors (P=0.0066). The overall difference between the early indoor vs late indoor crosses was greater than the difference between the late indoors vs late outdoors. The interaction between family and the crossing environment was insignificant and the F-value was lower

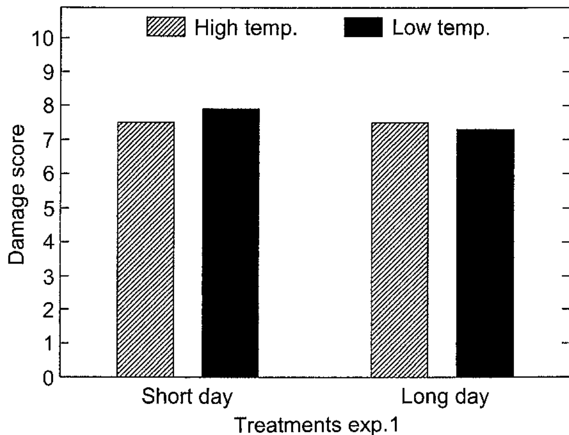

Fig. 2 The average frost damage from short- vs short-long-day pollen treatments as well as high- and low-temperature pollen treatments in experiment 1 (Table 1). The results presented are mean values of all test temperatures

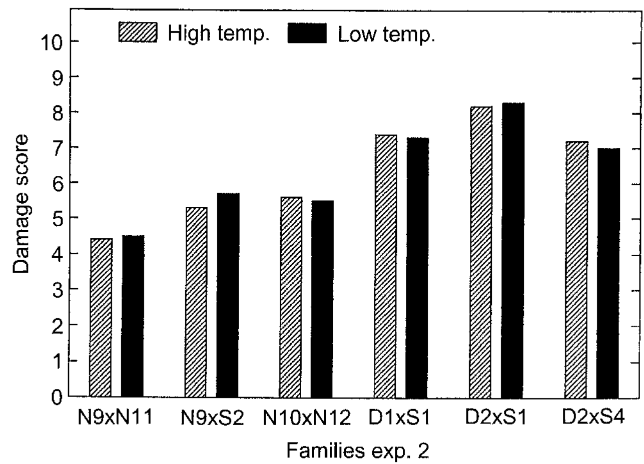

Fig. 3 The frost damage in six separate full-sib families and pollen treatments (Table 2) in experiment 2. The results presented are mean values of all test temperatures. Families (female×male) are named according to origin of the parents; N=Norway, S=Sweden, D=Dolina. Different *numbers* behind the same letter indicate that parents are unrelated

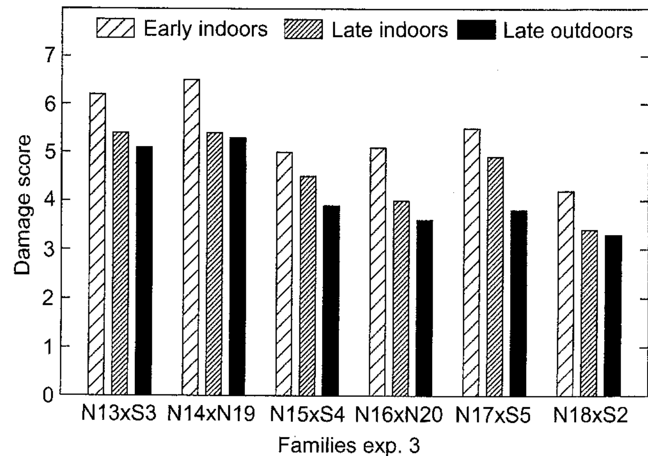

Fig. 4 The frost damage in six unrelated full-sib families as affected by the three female flowering environments (Fig. 1) in experiment 3. The results presented are mean values of all test temperatures. Families (female×male) are named according to origin of the parents; N=Norway, S=Sweden. Different *numbers* behind the same letter indicate that parents are unrelated

Table 3 The analysis of variance of frost damage, experiment 3 (transformed values)

Source	*df*	MS	F-value	P-value
Family (F)	5	1.16	27.4	0.0001
Crossing environment (CE)	2	1.57	47.8	0.0001
F × CE	10	0.03	0.8	0.6494
Test temperature (T)	5	4.36		
Replicate/T	54	0.09		
Error	959	0.04		

than 1.00 (Table 3). Exactly the same conclusions concerning the results of experiment 3 were reached using the residuals as the error term.

Discussion

The present data indicate that the effects of the parental environment on progenies of Norway spruce reported earlier (Johnsen 1988, 1989 a, b; Johnsen et al. 1989; Johnsen and Østreng 1994; Kohmann and Johnsen 1994; Skrøppa 1994; Skrøppa et al. 1994; Johnsen et al. 1995) are mainly influenced by environmental signals transduced at some stages during the reproductive process taking place in the female flowers. Thus, female meiosis, pollen tube growth, syngamy, early embryogenesis, embryo competition, and perhaps late embryo development (Owens and Blake 1985) could be one or several of the stages sensitive to the environmental factors. Thus, we can exclude the possibility that male meiotic drive and pollen selection during pollen maturation in the male flowers could be a significant biological factor explaining the observed effect of the reproductive environment on progeny performance in Norway spruce.

Results in experiment 3 confirm the hypothesis that flowering in an early and warm spring produces less hardy progenies than a late and cold spring (Kohmann and Johnsen 1994; Johnsen et al. 1995). The females accumulated more heat at a shorter photoperiod in the early crosses than in the two late treatments (see Fig. 1). However, the two late-crossing environments differed in accumulated heat, but very little in photoperiod. Thus, temperature is perhaps the most likely environmental factor triggering the process, but photoperiod cannot be excluded until we know whether a sensitive stage occurs early or late in reproduction. A more precise timing of photoperiodic and temperature treatments to the various reproductive stages in the female cones is needed to reveal the stages which are sensitive to environmental influence, and to find out whether the phenomenon is triggered only by temperature or photoperiod or by an interaction between these two climatic factors. If the developmental stages are found, a search for mechanisms can be initiated.

The environmental signal is transduced during sexual reproduction in the female flowers. However, the nature of this particular signal transduction (see Bowler and Chua 1994) and how it exerts its influence at the molecular level is unknown. Our data indicate that the effect of the crossing environment is persistent in the progeny. Thus, the mechanism should in our opinion operate either at a genetic (change in gene frequency caused by selection, or rapid genomic changes) or an epigenetic (gene regulation altered by imprinting) level (see Skrøppa and Johnsen 1994). The reproductive process offers several possibilities for directed selection. However, the potential effect of gametophytic and sporophytic selection is rather limited due to the low number of pollen grains in each pollen chamber and of embryos in a developing seed of spruce (Owens and Blake 1985). Thus, unless the selection proceeds in the same direction in a three-stage sequence (megaspore degeneration, pollen- and embryo-competition), it can hardly account for the observed effects reported.

Virtually no information is available about rapid genomic changes or epigenetic effects in trees. Interestingly, Meyer et al. (1992) found that environmental factors influenced 35*S* promotor methylation of a maize A1-gene construct in transgenic petunia and its colored phenotype. While blossoms on field-grown plants flowering early in the season were predominantly red, later flowers on the same plants showed a weaker coloration. The reduction of the A1-specific phenotype correlated with methylation of the 35*S* promotor. Moreover, they found that the stability of pigmentation correlated with the time of seed production. The A1-gene construct was rather insensitive to DNA methylation in progeny from flowers of young parental plants produced early in the season, but became susceptible to methylation within progeny from subsequent later crosses. So far, we can only speculate that such gene regulation, caused by activation or de-activation of certain genes by environmental conditions during reproduction, regulates the phenotypic expression of adaptive traits in Norway spruce.

Traits related to the phenology of Norway spruce provenances are clinally correlated with the latitude and altitude of the seed origin. As much as 60–93% of the variation has been explained by these parameters for traits such as bud set in the autumn, cessation of leader growth, duration of the growth period, and the development of autumn frost-hardiness (Dormling 1979; Skrøppa and Magnussen 1993; Dæhlen et al. 1995). Regardless of the type of mechanism involved, our results indicate that phenotypic provenance variation is not only caused by natural selection, but is also directed by environmental signals received by the female parent during sexual reproduction. Both processes seem to change phenology traits of the progeny in the same direction, and may explain why traits characterizing the annual growth cycle of Norway spruce provenances show such strong clinal variation along latitudinal and altitudinal gradients.

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