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Genotype by environment interactions for Norway spruce provenances and populations

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Genotype by environment interactions for Norway spruce provenances and populations

Samspill mellom genotype og miljø for provenienser og populasjonen av gran

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SUMMARY/SAMMENDRAG:

This report presents results from trials with populations from South and Central Norway and with provenances from Central Europe and Finland. The trials were both short-term planted on agricultural soil and field trials on forest sites. Measurements and assessments were made of height, bud flush and lammas shoots. Significant variation in these traits was present both among provenances, Norwegian populations and families within populations. For the Norwegian populations, interactions were present between trait means in the short-term and field trials. Large interactions were present between provenances and field trial sites located only a few kilometres apart for both survival and height. These interactions were most likely caused by differences in local temperature climate between these sites. Information about interactions, and whether they are predictable based om geographical and climatic variables, is important both for choosing appropriate provenances and for the breeding of Norway spruce.

Denne rapporten presenterer resultater fra forsøk med populasjoner fra Sør-Norge og Trøndelag og med provenienser fra Mellom-Europa og Finland. Både korttidsforsøk plantet på jordbruksmark og feltforsøk i skogen ble plantet. Målinger og registreringer ble gjort av høyde, tidlighet og høstskudd. Det var signifikante forskjeller i disse egenskapene både mellom provenienser, norske populasjoner og familier innen populasjoner. For de norske populasjonene var det samspill for middeltall av høyde og tidlighet i korttids- og feltforsøkene. Betydelige samspill for overlevelse og høyde ble

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funnet mellom provenienser og lokaliteter for feltforsøk som bare ligger noen få kilometer fra hverandre. Disse samspillene kom sannsynligvis på grunn av forskjeller i det lokale temperaturklimaet. Kunnskap om samspill og om de avhenger av geografiske og klimatiske faktorer, er viktig både for valg av provenienser og for planteforedlingen for gran.

LAND: Norge

GODKJENT /APPROVED	PROSJEKTLEDER /PROJECT LEADER
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1 Introduction

In Norway spruce (*Picea abies*), genetic variation is present among provenances (geographic regions), among populations within regions and among families within populations in traits related to climatic adaptation and for growth and quality, see review by Eriksson (2010). In trials in Norway, such variation has been expressed both among provenances originating from wide geographic areas (e. g. Fottland & Skrøppa 1989) and also among populations of more local origin (Dietrichson 1973; Skrøppa & Steffenrem 2019, 2020; Skrøppa 2021). The patterns of variation in phenology and growth traits are often clinal, related to the latitude and altitude of the origin of the provenance or populations (e. g. Dæhlen et al. 1995, Skrøppa & Steffenrem 2019, 2020). It has been assumed that natural selection has been an important factor in developing spruce populations adapted to differences in temperature climate and day length. Recent studies have shown that climatic conditions during seed production also may influence adaptive properties of Norway spruce, see review by Yakovlev et al. (2012).

When trees of the same provenances or populations are planted at sites with different environmental conditions for growth, then the ranking in performance among the genetic units may change and genotype by environment interactions are present. In the Nordic countries such interactions have been demonstrated for provenances (Fottland & Skrøppa 1989, Persson & Persson 1992), for families (Skrøppa 1984, Hannerz et al. 1999) and for clones (Karlsson et al. 2001). A successful choice of forest reproductive materials depends on reliable information about interaction effects, whether they are present, and if so, of critical environment factors. Such knowledge is essential in tree breeding, both for designing test procedures and for delineating zones for the use of genetically improved materials. If such interactions are predictable and can be related to site, climate and/or geographical factors then they are essential for obtaining gain in the breeding program (Hannerz et al. 1999, Berlin et al. 2015).

The intention with this report is to show the spatial scale at which genotype by site interactions in Norway spruce may operate. It is based on results from trials containing both materials from Norwegian populations and families obtained in a cone collection made in 1960 and introduced provenances from Central Europe and Finland. Measurements were made at age seven years from seed in one short-term trial planted on agricultural soil and in trials on forest sites at age 23 years. It will be shown that interactions between trial sites and provenances and populations may occur both when the sites are only a few kilometres apart or more distantly located.

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2 Materials and methods

The 1960 cone collections were made in 19 Norway spruce stands (populations) in the southern and central part of Norway (Dietrichson 1967). The intention was to collect cones from a maximum of 25 trees in each stand and keep the seed lots from each individual tree separate. Variation in seed quality reduced the size of the seed collection, but nearly 300 seed lots that could be used in trials were obtained. They were sown at Reiersøl Nursery, Agder, in 1962, in a randomized block design with four replicates (Dietrichson 1967). The seedlings were transplanted in 1964 at Hogsmark Experimental Farm, Ås, in a similar design. Two years later, in 1966, a short-term trial was planted at Hogsmark with seedlings from four seed lots (families) from each of 15 populations and 26 provenances from Central Europe and Finland. Measurements of height growth and phenology traits were made in this trial, and results at age seven years from seed were reported by Dietrichson (1969). He showed variation both among provenances, populations and among families within populations for most traits measured.

A combined provenance/progeny test was planted in 1966 at three forest sites in Hurdal (latitude 60°26') and at one site at Håheim, Etne, western Norway (latitude 60°40'), with the same families, populations and provenances that were planted in the short-term trial at Hogsmark. They originated from a large part of the distribution of Norway spruce in southern and central Norway and from Central Europe and Finland (Figure 1). The material included four open-pollinated families from each of 15 Norwegian populations from the 1960 seed collection and 26 provenances from Austria, Poland, Czech Republic and Finland (Table 1). The populations from southern Norway originated both from low and medium altitudes, and four were from altitudes 200 and 400 m in Trøndelag, central Norway.

Table 1. Provenances and populations planted in all trials. The Norwegian populations were each represented by four families.

Origin of populations/ provenances	Altitude m	Number of populations/ provenances
Southern Norway	0 - 160	6
Southern Norway	390 - 430	5
Trøndelag	200 - 400	4
Austria	950 - 1300	6
Poland	150 - 900	5
Czech Republic	550 - 950	8
Finland	50 - 130	7

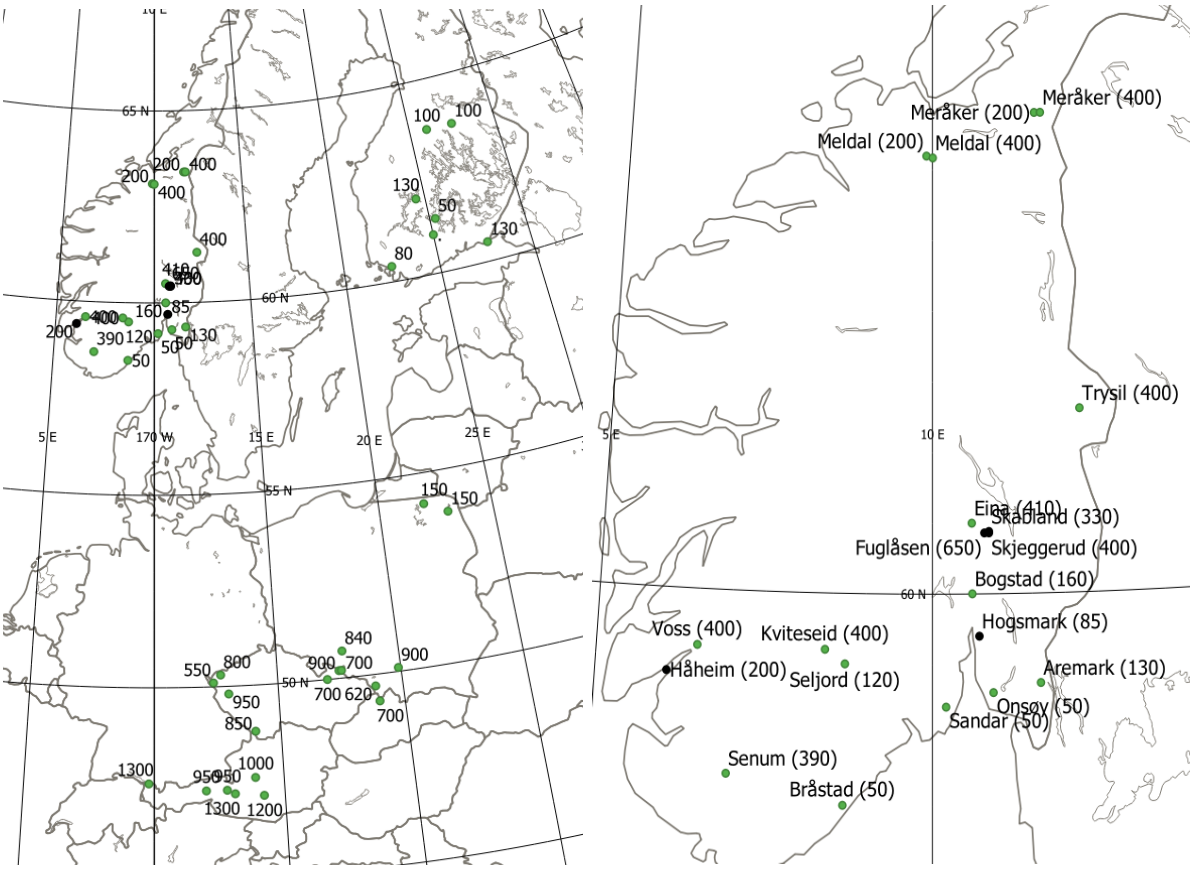

Figure 1. Populations and provenances planted at trial sites at Hogsmark, Hurdal and Håheim. Altitude is shown for each genetic entry (green dots) and sites (black dots).

The trials at Hurdal were planted at three different sites: Skabland, Skjeggerud and Fuglåsen, all within 2-3 km distance. The introduced provenances, the southern Norwegian and the Trøndelag populations were planted in different sub-blocks at each site. In each sub-block four trees of each entry (family or provenance) were planted in a plot at 2 m spacing in a randomized design. At Skabland, six blocks were planted, whilst five blocks were planted at the two other sites. The local climatic conditions were very different at the three sites. The Skabland site is in the flat terrain and is exposed to frost, while the two other sites are located on slopes without severe frost problems. The trial at Håheim was planted with four-tree plots in 16 blocks. Local temperature records were not available for these sites but mean annual temperature estimates based on observational gridded datasets (Lussana et al. 2019) for the period 1961-1990 are 2.8, 2.5 and 0.9 degrees for Skabland, Skjeggerud and Fuglåsen, respectively. Most likely, these means do not reflect the actual temperature climate at each sites as influenced by the very local topographical conditions. Mean annual temperature estimates for the period 1961-1990 are 5.3 and 5.1 degrees for Hogsmark and Håheim, respectively.

At the Hurdal sites, assessments of bud flush were made in 1968, based on Langlet's (1960) scale, in which high values means an early bud flush, heights were measured in 1968, 1975, 1980 and 1984 and assessments were made these years of double stems/leaders and ramicorn branches. At Håheim, height was measured in 1984, and a study of variation in wood density was made with material from this trial (Hylen 1997). Phenotypic and genetic relationships between traits measured in the short-term trial at Hogsmark and wood density components were published by Skrøppa et al. (1999).

From the short-term trial measurement and assessment data from age seven years of height, bud flush and lammas growth are available and will be related to measurements made at the Hurdal sites.

Means were calculated for populations and provenances at each site and analyses of variance were made to test for significance of differences in height and flushing scores both within and across sites.. Results of the tests are reported by p-values. Pearson correlations were calculated between means, both within and among sites. Means were also calculated for groups of populations based on altitude and of provenances, based on country of origin. Statistical analyses were made in SAS (SAS Institute 2003).

3 Results

3.1 Norwegian populations

The mean mortality of the populations in the period 1968 to 1984 at the three sites at Hurdal was 37.0 % at Skabland, 12.2 % at Skjeggerud and 15.6 % at Fuglåsen. At Skabland, the range in mortality was from 19.8 % to 56.6 % among the 11 populations from southern Norway and with lowest mortality percentages for the provenances from Trøndelag. A large proportion of the trees at this site showed injuries due to spring frost when they were examined in the summer of 1975 (assessment data not available).

Table 2. Trait means of Norwegian populations in the short-term trial at Hogsmark, at Håheim and total means at three sites at Hurdal. Below, the mean values of three groups of populations.

Populations/ altitude	Height 1968 Hogsmark cm	Height 1984 Hurdal cm	Height 1984 Håheim cm	Bud flush 1968 Hogsmark score	Bud flush 1968 Hurdal score	Mortality 1968-84 Hurdal %	Lammas shoots Hogsmark %
Senum 390 m	62	422	580	1.9	2.4	25.0	32.0
Bråstad 50 m	62	391	535	2.5	2.6	17.0	27.0
Seljord 120 m	70	452	504	1.5	1.7	32.1	24.6
Voss 400 m	54	387	544	2.4	3.2	17.9	10.9
Kviteseid 400 m	58	400	559	2.2	2.6	26.7	19.1
Bogstad 160 m	65	427	513	2.3	2.8	27.5	39.5
Onsøy 50 m	68	383	560	1.9	1.9	26.2	41.8
Sandar 50 m	62	423	534	2.2	2.6	17.3	28.1
Eina 410 m	63	435	541	1.6	2.2	16.8	16.4
Trysil 400 m	56	443	535	1.8	2.7	19.6	9.4
Aremark 130 m	67	421	574	2.9	3.0	31.6	58.6
Meråker 200 m	54	464	518	1.8	2.8	14.8	5.7
Meråker 400 m	47	399	516	1.9	2.8	23.0	2.3
Meldal 200 m	55	405	560	2.1	3.1	20.4	5.9
Meldal 400 m	44	418	510	2.1	3.0	16.2	3.1
Southern Norway:							
6 populations <160 m	67	416	537	2.2	2.4	25.3	36.6
5 populations >390 m	59	418	552	2.0	2.6	21.2	17.6
Trøndelag:							
4 populations	50	422	526	2.0	2.9	18.6	4.3

The range of variation in mean height in 1984 among populations at Hurdal was from 383 cm to 464 cm, with the highest mean for the Meråker population from altitude 200 m (Table 2). In the analysis of variance of height across the three sites at Hurdal the differences among populations were not significant (p=0.20), and there were no interactions were between sites and populations. Small, but significant differences were present among families within populations (p=0.05) and some interactions between sites and families (p=0.03). The means of the populations from the two altitude levels in southern Norway and the Trøndelag populations were of similar value. This was different from the heights in the short-term trial where the lowland populations were tallest and the Trøndelag populations had considerably lower heights (Table 2). There was a higher correlation between height in the short-term and field trials for the populations from above 390 m (r=0.91) than for the lowland populations (r=0.59). The populations with the tallest mean height at Hogsmark had the highest mortality at Hurdal (r=0.61). These populations also had the highest frequency of lammas shoots in the short-term trial. At all three sites at Hurdal small differences were present among populations and families for the percentage of trees with double stems and ramicorn branches.

At Håheim, the difference among populations in mean height 1984 was not significant (p=0.13), but there were also here significant differences among families within populations (p=0.03). At the population level, there were no relationship between the heights at Håheim and Hurdal (r=-0.39), nor between heights at Håheim and at Hogsmark (r=0.29).

For bud flush 1968 at Hurdal, significant differences were present both among populations (p=0.001) and among families within populations (p<0.0001), and there were no interactions between sites and populations or families. In the analysis of variance combining the Hurdal and Hogsmark trials a significant interaction was present between sites and populations (p<0.001). The main cause was that the trees of the four Trøndelag populations that flushed quite early in Hurdal had a bud flush approximately at the same days as the southern Norwegian populations at Hogsmark.

3.2 Provenances

The mean mortality in the period 1968 to 1984 was high at Skabland, 60.3 %, and was 20.2 % at Skjeggerud and 15.8 % at Fuglåsen. The Central European provenances had at Skabland a mean mortality twice the mortality of the populations from southern Norway. At Skjeggerud, less than 2 km away, the mean mortality of the provenances from Norway and Central Europe was quite similar. Here, the mean height of the trees from Poland was 37 % above the mean of the trees of Norwegian origin. At Skabland, the surviving trees of local origin were on average 12 % taller than those from the Polish and Czech origins. These results, presented in Figure 2, show that changes in the ranking of provenances for both mortality and height occur over short distances when differences in local climatic conditions are present.

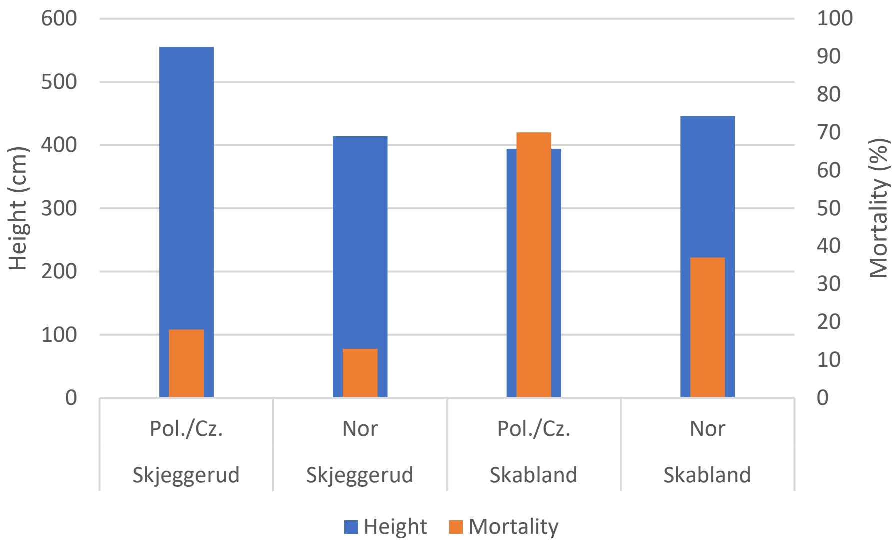

Figure 2. Means of Norwegian populations and provenances from Poland and Czech Republic for mortality and height at Skjeggerud and Skabland.

There were significant differences ($p=0.03$) between countries of origin for height measured in 1984 at Hurdal, but not between provenances within countries. The provenances from Finland had a significantly ($p<0.0001$) earlier bud flush in 1968 than those from the other countries, and those from Poland were the latest to flush (Table 3). At Hogsmark, the provenances from Finland had a timing of bud flush more like those from the other countries. The variation among provenances within countries for bud flush was not significant. The provenances from Poland and the Czech Republic performed generally better than those from Austria, whilst those from Finland had high survival and good growth.

At Håheim, the ranking of the country height means was the opposite of that in Hurdal, with the tallest trees from Austria and the lowest mean height for Finland. Austria had the highest mortality (28.6 %) and Finland the lowest (17.2 %).

Table 3. Means of provenances from Austria, Poland, Czech Republic and Finland in the short-term trial at Hogsmark, at Håheim and total means at three sites at Hurdal.

Country	Height 1968 Hogsmark cm	Height 1984 Hurdal cm	Height 1984 Håheim cm	Bud flush 1968 Hogsmark score	Bud flush 1968 Hurdal score	Mortality 1968-84 Hurdal %	Lammas shoots Hogsmark %
Austria	68	383	666	2.4	2.6	39.4	70.7
Poland	73	465	620	1.8	1.8	37.6	58.2
Czech Republic	76	422	658	2.0	2.1	32.1	69.8
Finland	56	455	548	2.4	3.1	19.2	23.8

4 Discussion

A major result from these trials is the large interactions between provenances and sites that may occur over short distances when there are climatic differences caused by changes in topography. The flat terrain close to the lake at Skabland is a “frost pocket” where frost events most likely take place the whole year, even if the estimated annual mean temperature is slightly higher than at Skjeggerud. These interactions were observed both for mortality and tree heights, and they were substantial for Central European provenances when compared with those of local origin. Such interactions were earlier reported between localities in Norway by Fottland and Skrøppa (1989), in Sweden by Persson & Persson (1992) and between Nordic sites by Skrøppa and Steffenrem (2021). In these studies, provenances were tested at sites with very diverse climatic conditions and located several hundred kilometres apart. When provenances were selected for reasonable growth capacity and grown in South Sweden and Denmark between latitudes 56 and 58 °N, low levels of interactions were present (Karlsson et al. 2001). For breeding populations in southern Sweden genotype by environment interactions were found to be small or moderate and rather unpredictable based on geographical and climatic variables (Berlin et al. 2015). These authors stated that effects of late spring frost damage could cause such interactions.

Genotype by site interactions for height were also observed between the short-term test site Hogsmark and the three sites in Hurdal both for provenances, the Norwegian populations and also for families within populations. The interactions were not due to age effects since the correlations between height at different ages in Hurdal were high. They were larger for the populations from low altitude in southern Norway than those from higher altitudes or from Trøndelag. Populations from the former region had the best height growth at Hogsmark, but not in the field tests. Similar interactions were also present between Håheim and Hogsmark and Håheim and Hurdal. An implication of these results is that tests of populations or families to be used in reforestation or tree breeding for at sites at medium or higher altitudes should not be done at a lowland site like Hogsmark. However, positive relationships for both populations and families have in other studies been found between height growth at Hogsmark and field trials (Skrøppa 2021; Solvin 2020). Most likely the climatic conditions were better at these field trial sites compared to those at Hurdal, and also the temperature climate has been less severe during the last 30 years compared to the period before.

The timing of bud flush in spring is a trait that varies both at the provenance, population and family level. Generally, Norwegian populations from northern latitudes or high altitudes will have the earliest bud flush (e. g. Skrøppa & Steffenrem 2019, 2020). The populations within the two altitude zones in southern Norway varied considerably for the timing of bud flush but had on average the same mean scores both at Hurdal and Hogsmark. The Trøndelag populations performed differently with medium scores at Hogsmark and flushed earlier than the southern Norwegian populations in Hurdal. This interaction could be due to the transfer from Trøndelag to warmer temperature conditions at Hogsmark and colder temperatures more like those in Trøndelag in Hurdal. A similar interaction was observed for the Finnish provenances with an early bud flush at Hurdal and later at Hogsmark. These effects could be caused by higher temperatures at Hogsmark in the autumn, as it has been shown that high temperatures during the dormancy period may delay bud burst the next spring (Heide 1974, Granhus et al. 2009). The Trøndelag populations could be more influenced by such effects.

These results provide useful information for the breeding of Norway spruce. The large variation within populations initially observed in the short-term test, which later has been demonstrated in several studies, stressed the need for progeny testing of candidate trees for the breeding populations. However, information from such tests at low altitude locations may not be appropriate when the intention is to select materials intended for planting at higher altitudes. A similar statement was given by Skrøppa & Steffenrem (2019) for tree breeding in the Trøndelag region.

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Norsk institutt for bioøkonomi (NIBIO) ble opprettet 1. juli 2015 som en fusjon av Bioforsk, Norsk institutt for landbruksøkonomisk forskning (NILF) og Norsk institutt for skog og landskap.

Bioøkonomi baserer seg på utnyttelse og forvaltning av biologiske ressurser fra jord og hav, fremfor en fossil økonomi som er basert på kull, olje og gass. NIBIO skal være nasjonalt ledende for utvikling av kunnskap om bioøkonomi.

Gjennom forskning og kunnskapsproduksjon skal instituttet bidra til matsikkerhet, bærekraftig ressursforvaltning, innovasjon og verdiskaping innenfor verdikjedene for mat, skog og andre biobaserte næringer. Instituttet skal levere forskning, forvaltningsstøtte og kunnskap til anvendelse i nasjonal beredskap, forvaltning, næringsliv og samfunnet for øvrig.

NIBIO er eid av Landbruks- og matdepartementet som et forvaltningsorgan med særskilte fullmakter og eget styre. Hovedkontoret er på Ås. Instituttet har flere regionale enheter og et avdelingskontor i Oslo.

Forsidefoto: Tore Skrøppa, NIBIO. Forsøk i Stor-Elvdal med familier fra populasjonene Eina og Trysil plantet 1967. Foto fra 2019.

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