

Diallel crosses in *Picea abies* III. Variation and inheritance patterns in nursery trials

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Abstract

The complete diallel cross is the only mating design that provides estimates of variance components of general combining (GCA), specific combining ability (SCA), maternal and reciprocal effects, in addition to heritabilities and genetic correlations. To obtain such estimates, complete diallels were made among 10 trees in each of three natural Norway spruce populations from altitude 300 and 500 m in Norway. Nursery trials were performed with the families from these crosses and families from seeds collected from open pollination. Traits measured and analysed are seed weight, germination rate, germination percentage, terminal bud set, and seedling heights the first and second years. The seedlings from the population at origin 500 m had lower seed weight, lower heights and earlier bud set than those from the two populations from lower altitude. A considerable variation was present among families within each diallel, and the GCA variance components had the highest values and were significant for most traits. Variance components for SCA and maternal effects were also significant for some traits, but with inconsistent values in the three diallels. A strong relationship was present between the weight of the seed lots from the maternal parent and mean family height after one and two growing seasons. The highest estimate of heritability was observed for bud set, with similar values in all three diallels.

Keywords: *Norway spruce; germination; height growth; bud set; maternal effects; heritability*

Introduction

The genetic variability of quantitative traits in Norway spruce (*Picea abies* (L.) Karst), which is the most important commercial forest tree species in Northern Europe, has been characterized in many studies. Eriksson (2010) published a comprehensive review of results from the genetic research in the species during the period 1990-2009. The studies show that for most traits considerable variation is present among populations from different latitudes and altitudes (König 2005, Jansson et al. 2013), and clinal variation has been demonstrated for adaptive traits (e. g. Krutzsch 1974, Modrzynski 1995, Hannerz et al. 2003). Genetic variation is also present among families, both from natural and from breeding populations (e. g. Ekberg et al. 1985, Kroon et al. 2011). Estimates of genetic variance components, heritabilities and genetic correlations have been published based on measurements in progeny tests (e. g. Kroon et al. 2011). Heritabilities estimates generally show low to medium values for growth traits and quite high values for growth rhythm traits, such as the timing of bud flush in the spring (Hannerz et al. 1999).

Many of the studies presenting estimates of genetic parameters in Norway spruce are based on progeny tests where parents are selected plus-tree originating from different provenances or populations (e. g. Kroon et al. 2011, Berlin et al. 2019). Thus, the patterns of genetic variation among trees within natural populations cannot be separated from that among provenances or populations. In contrast to these studies, our aim was to characterize the natural genetic variation and inheritance patterns within populations. Therefore, as part of the genetic architecture studies in the species, a complete diallel cross was made on standing trees in each of three natural populations of Norway spruce. This report presents results from nursery trials up to age 2 years with the families from the three diallels.

The complete diallel, involving each parent both as mother and father in all possible cross combinations, is a mating design that provides sets of reciprocal full-sib families (Möhring et al. 2011, Isik et al. 2017). In the analyses of measurements from trees in complete diallels, the observed variation among and within families can be decomposed into several variance components. Estimates can be made of components due to general combining (GCA) and specific combining ability (SCA) effects (Möhring et al. 2011, Isik et al. 2017). Furthermore, information can be provided whether reciprocal effects are important, and partitions can be made of variance components due to maternal (general reciprocal) and non-maternal (specific reciprocal) effects (Cockerham and Weir 1977). Such information is important for the development of breeding strategies for a species (e. g. Wu and Matheson 2001). The genetic interpretation of the components will depend on several assumptions (Gilbert 1958, Baker 1978), which are difficult to verify. Complete diallels are rarely made with forest trees due to the large number of crosses needed.

Few studies on diallel crosses with forest trees have been published compared to those with agricultural crops. In a 7 x 7 complete diallel with *Picea mariana* with results from seedlings in the first two growth seasons, Morgenstern (1974) found that the GCA variance component was the dominant component of genetic variation, but some maternal components were observed for germination traits and early heights. Van Wyk (1976) observed maternal effects for three months' height in a diallel with *Eucalyptus grandis* and that the SCA component was important at the very young age. These effects disappeared at later ages, and he found that the GCA variance component was significant for most traits. The general trend from analyses of traits measured at young ages in other diallel trials (Snyder and Namkoong 1978, Samuel 1991, Blada 1999) is that the GCA variance components has the highest value and that SCA and maternal components may be present at young ages and become smaller when the trees get older.

Results from analyses of seed yield and seed weights of the families in the three diallels have been presented earlier (Skrøppa and Tho 1990), as have the performance and inbreeding depression of the selfed families (Skrøppa 1996). A large variation was found among maternal parents for filled seed percentages and seed weight. Similarly, the level of inbreeding depression varied among the selfed families.

The objective of this report is to present and discuss the relative importance of the different genetic variance components and estimates of heritability and genetic correlations provided by the analyses of the complete diallels for germination traits, height ages 1 and 2 years and terminal bud set measured in the nursery trials.

Materials and Methods

Materials

In each of three natural populations of Norway spruce ten randomly selected trees having both female and male flowers and standing more than 50 m apart, were in the spring of 1973 crossed in all combinations, including both reciprocal crosses and self-pollinations. Thus, one complete diallel cross was made within each population. The age of the trees varied from 40 to 96 years. Details describing the populations and the crossing procedures were presented by Skrøppa and Tho (1990). The three populations were all located at different altitudes in the same region at latitude 61°N in south-eastern Norway, less than 60 km apart. Geographic locations and climatic data for the populations are presented in Table 1. The sets of families generated by the crosses in the three populations will be denoted by Diallel 1, 2 and 3, respectively.

All outcrossed families in Diallel 1 produced filled seeds, while two failed to do so in Diallel 2. The dimension of Diallel 3 was reduced to 9 x 9 due to the non-functioning pollen from one of the parents (Skrøppa and Tho 1990). All outcrossed families in this reduced diallel produced filled seeds. The cones for the full-sib families (FS) from the controlled crosses were kept in the paper bags used for isolation until they were collected in early October. At the same time, cones from open pollination (OP) were collected from all parents. During seed extraction and cleaning all seed lots were given the same treatments. The 1000 seed weight of filled seeds from each family was determined (Skrøppa and Tho 1990).

Nursery trials

Filled seeds from both outcrossed and selfed families were sown and germinated in multi pot containers in March 1974 in the greenhouse at Hogsmark Experimental Farm (Table 1), Ås, and the containers were then kept in cold storage for four weeks. Germination and initial growth took place in an unheated greenhouse for the first two months until the seedlings were moved outdoors on June 18. The seedlings were grown in the containers for two growing seasons in six replicates of family plots of 31-32 sown seeds. Each diallel was kept as a separate unit during the cultivation which followed standard nursery routines as regards watering and fertilization.

In the nursery, early germination was assessed after 10 days, and a final germination record was made after 35 days. The germination rate (GR) was calculated per family plot in each replicate as the percentage of seeds that had germinated after 10 days based on the total number of seeds sown, and the germination percentage (GP) after 35 days. The heights of 15 seedlings growing in the centre rows of each family plot were measured at the end of the first (H1) and second growing season (H2) to the nearest 0.5 cm. At the end of the second growing season in the last week of September, each seedling in three replicates was visually examined for visible apical bud, and the percentage of seedlings with terminal buds was calculated (BS2).

Table 1

Geographic origins and climatic characteristics of the three populations where the diallel crosses were made and of the Hogsmark Experimental Farm. Climatic values are averages for the period 1961-1990 and are from MET Norway (Lussana et al. 2019).

Diallel	Population	Latitude	Longitude	Altitude	Annual mean temperature	Temperature sum degree days
1	Veldre	60°58'	10°56'	500 m	1.1 °C	740
2	Gjøvik	60°50'	10°38'	270 m	2.4 °C	1000
3	Braskereidfoss	60°47'	10°50'	300 m	2.0 °C	960
Trial	Hogsmark	59°40'	10°43'	85 m	5.4 °C	1400

A second sowing of remaining seed lots from the outcrossed families from Diallels 2 and 3 was made in the spring of 1986 in the same nursery, and germination and plant cultivation were done following the same routines as described above. Assessment of terminal buds were performed on four occasions during August the same year, and the cumulative percentage of seedlings per plot that had formed terminal buds at each date was calculated (BS1). The statistical analyses of BS1 are based on the bud set percentages at the day with the largest variation among families which occurred on August 25.

Calculations, statistical analyses and parameters

All statistical analyses were made within each diallel and reported separately.

The plot percentages of GR, GP and BS were transformed by the arc sin square root transformation, and statistical analyses were performed based on the transformed values. The analyses of BS for Diallel 1 were based on the assessments made in the nursery trial in 1975 at the end of the second growing season (first sowing of the material). For Diallels 2 and 3, the transformed BS from the 1986 nursery trial (second sowing) were used in the statistical analyses, as the assessment of the seedlings in these two diallels were made at a too early date after the first sowing, with a mean bud-set percentage lower than 10 %.

Analyses of heights at ages 1 and 2 years (H1 and H2) were based on plot means of 15 seedlings. Thus, the error term in these analyses was the sum of a random plot effect and the within-plot individual error term divided by the number of individuals (15) measured in the plot. Estimates of the within-plot variance components were provided in separate analyses, and thus also the plot variance components could be estimated.

Analyses of the measurements made of the outcrossed (FS) diallel families were made with the ASReml-R software (Gilmour et al. 2006; Butler et al. 2017; see also Isik et al. 2017), based on a completely random model with reciprocal effects described by Möhring et al. (2011), with references to Cockerham and Weir (1977). For the plot mean of block k in the cross between parents i (female) and j (male), the model was

$$Y_{ijk} = \mu + GCA_i + GCA_j + RGCA_i - RGCA_j + SCA_{ij} + \beta_{ij} RSCA_{ij} + B_k + E_{ijk}$$

Here, μ is the common population mean and B_k , E_{ijk} are block effects and error term, respectively, GCA_i and GCA_j are the general combining abilities of parents i and j , $RGCA_i$ and $RGCA_j$ are the reciprocal parental or maternal effects, SCA_{ij} is the specific combining ability of parents i and j , $RSCA_{ij}$ is the specific reciprocal cross effect and $\beta_{ij} = 1$ for $i < j$, $\beta_{ij} = -1$ for $i > j$. In the ASReml analyses all effects were assumed to be random and be independent and normally distributed with mean 0 and variances σ^2_{GCA} , σ^2_{RGCA} , σ^2_{SCA} , σ^2_{RSCA} , and σ^2_{E1} , respectively, for the general combining ability (GCA), the reciprocal parental (RGCA), the specific combining ability (SCA), the reciprocal cross (RSCA), and the error (E) effects.

The genetic effects of a cross will then have variance $\sigma^2_G = 2\sigma^2_{GCA} + 2\sigma^2_{RGCA} + \sigma^2_{SCA} + \sigma^2_{RSCA}$. The phenotypic variance component, σ^2_{phen} , was estimated by adding the estimate of the error variance component to the estimate of σ^2_G . The narrow sense heritability was estimated as $h^2 = 4\sigma^2_{GCA}/\sigma^2_{phen}$. Such estimates are presented with their standard error even if the GCA variance components are not significant.

The ASReml analyses provide estimates of the different variance components, and the narrow sense heritability was calculated as $h^2 = 4\sigma^2_{GCA}/(\sigma^2_G + \sigma^2_P + \sigma^2_E)$. The standard errors of the estimates were calculated by first order Taylor series approximation by the ASReml-R software (Gilmour et al. 2006; Butler 2009).

The GCA coefficient of variation was calculated in percentage as $CV_A = 100(2\sigma_{GCA}/\bar{Y})$, where $\bar{Y}$ is the trait mean. It was only calculated for heights, diameter, DAYS and RSE.

The ASReml analyses provided breeding values (BLUP) for the parents. Pearson correlations were calculated between the breeding values of each trait to obtain proxy estimates of genetic correlations between traits. Similar correlation coefficients were calculated between the breeding values and seed weights. Genetic correlations were estimated from bivariate ASReml analyses for six pairs of traits. In all cases, these estimates had slightly higher absolute values than the Pearson correlation coefficients between the BLUP estimates of the same traits.

Significance tests of the variance components can be made by the ratio of the variance component to its standard error (Z-test) provided by ASReml output. More powerful tests of whether the variance component is significant different from zero can be made by the likelihood ratio test, performed by deleting the factor of interest from the model and compare

this with the likelihood of the full mixed model including the tested component (Isik et al. 2017). This was done for some of the traits measured and comparisons made with the corresponding Z-value. They showed that the likelihood ratio test in most cases was significant when the Z-value had higher values than 1.2-1.3. Differences between the fixed effects in the models were tested by the Wald statistic provided by the ASReml analyses.

Analyses of variance were performed for families after open pollination (OP) for the same traits measured for the full-sib families. BLUP predicted values were calculated for each parent in the diallel and for maternal parents based on the OP families. All analyses were made separately for each diallel.

Results

Phenotypic variation

The mean performance of the full-sib families from the three diallels differed for most traits (Table 2). The families of Diallel 3 had on the average a faster rate of germination (70 %) than those of the two other diallels (56 and 65 %), but all had a similar mean germination percentage in the range of 92-95 %. For early height growth, the seedlings of Diallel 1 were shorter than those of the two other diallels, with mean heights of 55 (H1) and 197 mm (H2), compared to 67 and 238 and 70 and 269 mm, for Diallels 2 and 3, respectively. The mean diallel bud set percentages at the end of the second growth season in 1975 were 30, 10 and 6 %, confirming provenance differences in this trait between populations from altitudes 300 and 500 m. At the second bud set assessment in 1986, the mean bud set curves of families of Diallels 2 and 3 were similar (not shown).

Within each diallel a substantial variability was observed among full-sib and half-sib families for all traits. As examples, the ranges of variability among full-sib family means of Diallel 1 were from 26 to 93 % for GR, from 147 to 253 mm for H2 and from 0 to 71 % in BS (Table 2). Within the two other diallels similar ranges of variation were present.

Variance components, heritabilities and correlation patterns

The results from partitioning into variance components and genetic parameters are summarised in Table 3. The estimates of the GCA variance component showed high values for most traits in all three diallels and had in most cases Z-values between 1.5 and 3 (Z-values not shown in table). Germination rate (GR) showed quite large RGCA and some SCA effects. GP showed low values of variance component estimates, except for RSCA, and low heritability values. SCA and RSCA effects were present for H1 and H2 in Diallels 1 and 2, but not in Diallel 3. The lowest values of heritability estimates, with estimates the same value as their standard errors, were found for GP. BS showed the highest estimate of heritability, with quite the same values in all three diallels. The heritability estimates were lower for H2 than for H1 in both Diallel 2 and 3, but the opposite was the case in Diallel 1. The plot variance components had

high values for H1 and H2 and contributed between 15 and 31 % of the total phenotypic variance, excluding the block component.

The estimates of the genetic correlations between these traits (Table 4) showed quite different values in all three diallels and were in most cases not significant. The strong negative correlation between BS and H2 ($r=-0.86$) in Diallel 1 should be noted. Both traits were measured at age 2 years in the same trial in this diallel. In the two other diallels, the genetic relationships between BS, assessed in a separate test 1986, and the other traits measured in the nursery trials in 1975, were weak. High values of genetic correlations were estimated between GR and GP in Diallel 1 and Diallel 2, but this relationship was weaker in Diallel 3 (Table 4). In Diallel 3, a positive genetic relationship was present between GR and seedling heights in both years.

A considerable variation between families in 1000 seed weights, and with a strong maternal component for this trait, has been reported earlier for this material (Skrøppa and Tho 1990). Within each diallel, seedling heights, particularly at age 1 (H1), but partly also at age 2 years (H2), were strongly related to the weight of seed lots from the maternal parent as shown in Figure 1. The correlation coefficients between the mean seed weight of the maternal parent and the mean of H1 of the maternal half sib family were $r=0.79$ and $r=0.77$ in Diallels 1 and 3. However, in Diallel 2 it was as low as $r=0.14$ for all the families but increased to $r=0.83$ when the aberrant parent 12 was excluded. For H2, the relationships to seed weight were still significant. The relationships with seed weight for GR, GP and BS were weak (data not shown).

Significant variation ($p<0.01$) was present between the OP families in all three diallels (analyses not shown). The FS families were on average slightly taller than the OP families in the nursery (H1 and H2) and this could be due to seed weight differences. The 1000 seed weight of lots of the FS families were on average 0.6 gram heavier than those from the OP families.

Pearson correlation coefficients were calculated between BLUP-predicted values for each parent in the diallel and in the OP families and had values 0.84, 0.78 and 0.86 for H1, and 0.89, 0.66 and 0.65 for H2, in the three diallels.

Discussion

Statistical and genetic considerations

The ten parents in each diallel should be considered a representative sample of the population, and the parameters estimated from their progenies should apply to the whole stand. However, as discussed by Skråppa and Solvin (2019), the estimates will have quite large sampling errors due to the small number of parents involved and due to experimental errors in the trial (Falconer and Mackay 1996; Lynch and Walsh 1993; Isik et al. 2005).

Table 2

Phenotypic means of each diallel and range of variation among full-sib families for the traits analysed. The number given in the acronyms are age from seed.

Trait	Acronym	Diallel 1, 500 m		Diallel 2, 270 m		Diallel 3, 300 m	
		Mean	Range	Mean	Range	Mean	Range
1000 seed weight (g)	SW	5.3	3.4 – 7.1	6.1	4.6 – 8.1	5.7	3.7 – 8.8
Germination rate (%)	GR	65	26 – 93	56	17 – 87	70	34 – 96
Germination percentage (%)	GP	92	69 – 99	93	72 – 100	95	79 – 100
Bud set age 1 (%)	BS1			49	6 – 91	44	16 – 78
Bud set age 2 (%)	BS2	30	0 – 71	10	0 – 43	5	0 – 21
Height ag 1 (mm)	H1	55	41 – 70	67	51 – 89	70	51 – 87
Height age 2 (mm)	H2	197	147 – 253	238	184 – 287	269	193 – 320

Table 3

Estimates of variance components, heritabilities and the coefficient of variation from the ASReml analyses of the traits measured in the nursery trials. Heritabilities for GR, GP and BS are estimated from plot-means, and for H1 and H2 from individual seedlings. Standard errors of estimates are presented in parentheses. Variance components are multiplied by 10^4 for GR, GP and BS.

Sources of variation	GR Germination rate	GP Germination percentage	BS1) Bud set	H1 Height year 1	H2 Height year 2
Diallel 1					
GCA	43 (24)	6 (5)	184 (96)	13.2 (6.7)	224.0 (112.0)
RGCA	28 (16)	7 (5)	4 (9)	0.2 (0.5)	8.3 (9.1)
SCA	21 (16)	1 (6)	28 (39)	5.0 (2.1)	39.3 (26.1)
RSCA	2 (11)	15 (9)	6 (34)	4.0 (1.8)	34.0 (24.5)
Block	200 (130)	30 (21)	176 (184)	10.5 (6.9)	172.8 (115.1)
Error plot	533	285	756	45.3	819.3
Plot				37.2	734.3
Error				130.5	1267.0
Heritability plot	0.25 (0.12)	0.08 (0.05)	0.63 (0.23)		
Heritability				0.26 (0.13)	0.35 (0.18)
CV _A				13.2 (3.4)	15.2 (3.8)
Diallel 2					
GCA	112 (58)	8 (8)	110 (59)	25.96 (12.8)	117.3 (63.3)
RGCA	57 (30)	4 (4)	19 (14)	0.0	0.0
SCA	27 (19)	36 (15)	61 (29)	3.84 (2.3)	12.6 (33.0)
RSCA	3 (13)	21 (12)	44 (25)	3.79 (2.0)	91.0 (45.6)
Block	221 (160)	0.0	46 (50)	28.54 (20.6)	79.0 (65.3)
Error plot	482	261	289	53.52	1172.8
Plot				41.98	1039.1
Error				173.2	2006.9
Heritability plot	0.53 (0.20)	0.09 (0.09)	0.67 (0.25)		
Heritability				0.38 (0.19)	0.14 (0.07)
CV _A				15.3 (3.8)	9.1 (2.5)
Diallel 3					
GCA	77 (44)	3 (4)	90 (53)	19.5 (10.2)	137.1 (77.7)
RGCA	41 (23)	1 (3)	8 (10)	6.6 (3.6)	25.7 (20.0)
SCA	39 (21)	11 (8)	40 (29)	0.8 (1.9)	21.1 (34.5)
RSCA	9 (13)	14 (9)	24 (24)	0.0	19.9 (33.6)
Block	259 (167)	40 (27)	119 (124)	46.0 (29.7)	37.9 (34.8)
Error plot	435	221	324	69.2	1217.7
Plot				57.5	1082.8
Error				175.4	2024.3
Heritability plot	0.43 (0.20)	0.05 (0.06)	0.62 (0.26)		
Heritability				0.27 (0.14)	0.16 (0.09)
CV _A				12.7 (3.3)	8.7 (2.5)

¹⁾BS assessed at age 2 in Diallel 1 and at age 1 in Diallel 2 and Diallel 3.

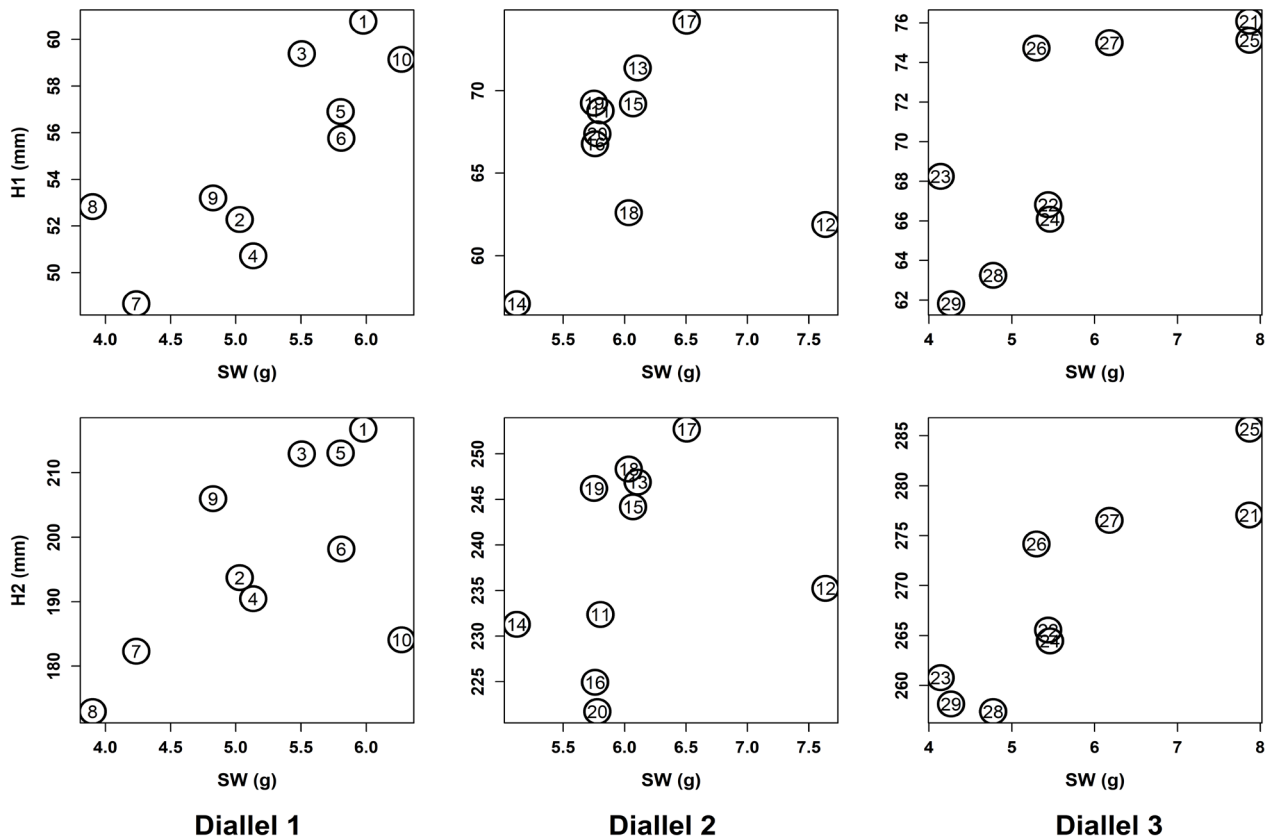


Figure 1

Plot of relationships between mean 1000 seed weight (SW) for the maternal parent against the mean height of maternal half-sib family year 1 (H1) and year 2. Parent trees are number 1 to 10, 11 to 20 and 21 to 29 in Diallels 1, 2 and 3, respectively.

Table 4

Estimates of genetic correlation coefficients based on BLU-predicted values. Estimates in Diallel 1 are in the first line, those in Diallel 2 are in the second line and those in Diallel 3 are in the third line. Absolute values larger than 0.63 or 0.77 are considered significant at the 5 and 1 % level, respectively, in Diallels 1 and 2, and larger than 0.67 and 0.80 in Diallel 3. These values are marked in bold fonts.

	GP	BS	H1	H2
GR	0.87	-0.54	0.31	0.40
	0.70	0.12	0.46	-0.13
	0.40	0.26	0.82	0.77
GP		-0.70	0.25	0.59
		-0.10	0.16	-0.25
		0.17	0.14	0.11
BS			-0.33	-0.86
			0.03	-0.08
			-0.19	-0.04
H1				0.49
				0.59
				0.87

Skrøppa and Solvin (2019) discussed the type of genetic interpretations that can be derived from the analyses of diallels with trees, which will depend on the assumptions made. One important issue, whether the relative magnitudes of variance components from quantitative genetic analyses indicate the relative importance of additive and non-additive gene actions has recently been questioned (Huang and Mackay 2016), see also Falconer and Mackey (1996). The analyses presented here partition the phenotypic variance into components predicting the resemblance between relatives and the short-term response to selection, information that is useful in tree breeding (Boyle 1987; Möhring et al. 2011). The analyses provide estimates of the relative amounts of GCA and SCA variances and whether there are any reciprocal parental (RGCA) or reciprocal cross effects (RSCA). In the classical quantitative genetic model, the GCA variance component represents one fourth of the additive genetic variance and the SCA component one fourth of the dominance genetic variance if epistatic genetic effects are not present or negligible (Huang and Mackey 2016). Presence of RGCA or RSCA effects may bias estimates of breeding values and genetic parameters estimated from families in standard mating designs used in tree breeding (Wu et al. 2001). Knowledge of such effects, provided from the diallels, are therefore

important for proper use of estimates of heritability and genetic correlations, which are important statistical parameters to be used when choosing strategies for Norway spruce breeding.

The estimates of genetic parameters from the families in the diallels represent the variability patterns in each of the three natural populations. In addition to the low number of parents, as discussed above, several other factors can influence the values of the estimates: such as the production routines of seedlings in the nursery, effects of transplanting and environmental variation within blocks due to soil and moisture conditions. Mistakes made by humans during the crosses and later when labelling seedlings and at planting may have occurred. The consistency between parameter estimates from two or three diallels, and from the open-pollinated families, will be crucial for drawing general conclusions. It will also be important to make comparisons with estimates from large progeny testing trials in practical tree breeding of Norway spruce, even if these families are from selected plus trees. It may also be the case that the three populations sampled do have different patterns of variation.

Variation and inheritance patterns

The differences in mean values that were observed for most traits of families from Diallel 1 and Diallels 2 and 3 confirm results from earlier studies of Norway spruce provenances from different altitudes both in southern Norway (Dietrichson 1967, 1969, 1973; Skråppa et al. 2007) and Mid-Norway (Skråppa and Steffenrem 2019) when tested in common garden trials. Seedlings from natural populations from low altitudes are taller in the nursery and also have a later terminal bud set than those from populations originating from higher altitudes. They also have a later terminal bud set. Similar results, with clinal variation related to either the mean annual temperature or the altitude of the populations, were recently presented by Skråppa and Steffenrem (2019) for Norway spruce populations in Mid-Norway. Differences between populations separated by 200 m in altitude, as we have here, were present for most traits. It should be noted that these results are observed at a site with more favourable conditions than at the origin of the natural populations (Table 1).

Germination rates and germination percentages in the nursery have been recorded and analysed only in a few trials (e. g. Morgenstern 1974; Bramlett et al. 1982; El-Kassaby et al. 1992). The early development characterized by these traits could be influenced by seed factors which have unbalanced contributions from the two parents (Skråppa and Tho 1990). Such factors are the seed coat, which is maternal diploid tissue, the haploid endosperm, which is inherited from the maternal parent, and the diploid embryo, where the male influence is found. For germination rate (GR), both GCA and RGCA variance components were significant in all three diallels, indicating both a general parental and a general maternal effect. For the germination percentage no such effects were present. In a 7 x 7 diallel with black spruce Morgenstern (1974) found similar results with the highest values for the GCA and RSCA variance components for germination rate. He found no GCA

component for germination percentage, but significant values for the other components. In a small diallel involving five parents of *Pinus virginiana* Bramlett et al. (1982) found that both GCA, maternal and reciprocal effects, but no SCA effects, influenced the germination response.

St. Clair and Adams (1991) presented variation in germination rate and germination percentage among open-pollinated families of Douglas fir and found low correlations to seed weight for these traits, similarly to what we found in the diallel families. In a study of families from seed orchard clones of the same species, El-Kassaby et al. (1992) concluded that germination speed in this species is under strong maternal control but found no relationships between seed weight and germination traits. Our results showing similar results for germination rate in Norway spruce as found for Douglas fir, indicate a maternal influence on this trait which is not expressed by seed weight. For germination percentage (GP) no such effect was found. The lack of relationships between seed weight and germination traits was observed already by Schell (1960) who, based on trials with Norway spruce, stated: "In single trees there exist no connection between 1000-seed-weight and germination energy."

The high values of the GCA variance component estimates for H1 and H2 in all three diallels indicate that the genetic variability of early height growth is to a large extent determined by additive genetic effects. The estimates of the variance components of RGCA, SCA and RSCA had lower values and their levels of significance were not consistent among the three diallels.

The seedlings in Diallel 1 had at both ages smaller size than those of the two other diallels and variable effects of competition among and within plots in the dense containers could be one reason for differences among the diallels in values of the variance component and in heritability estimates. In addition, our results demonstrate a maternal influence on these traits, not shown in the variance components estimates, but expressed by the relationships between H1 and H2 for the maternal half-sib families from the diallels and the mean seed weight of these families shown in Figure 1. Offspring from mothers that produce light seeds were shorter the first two years than those from mothers with higher seed weights. However, seedlings from some mothers producing heavy seeds may be shorter than expected, as demonstrated by the offspring from parent 12 in Diallel 2. Our results correspond with those found by Mikola (1989) who reported heights of half-sib families of Norway spruce from age 1 to 14 years and found high correlations between early heights and seed weights. In Douglas fir, positive relationships have been found between seed weight and early heights (Sorensen and Campbell 1993), but also that these relationships were weaker at age 2 than at age 1 years (St. Clair and Adams 1991).

Terminal bud set was assessed in Diallel 1 only at one date at the end of the second growth season and on four occasions during the first growth season in Diallels 2 and 3. This trait has been studied in provenances trials with Norway spruce seedlings and clinal variation both with latitude and altitude has been identified (e. g. Dormling 1973, Krutzsch 1986, Hannerz and Westin 2000). The results from our study, from Skråppa

(1991) with a subset of families from Diallels 2 and 3, and from Skråppa and Steffenrem (2019) show that there is considerable genetic variation for this trait also within natural populations and that the GCA variance component has the highest value. Significant GCA variance components were also found for this trait by Eriksson et al. (1978) for seedlings from different provenances grown in growth chambers. It is remarkable that the heritability estimates in the three diallels were quite similar for the bud set assessments made at the end of the second growth season in Diallel 1 and the first growth season in Diallel 2 and 3.

In the analyses of heights at ages 1 and 2 years of seedlings of the selfed families, strong relationships were found between the selfed and outcrossed progenies in Diallel 1, but not in Diallels 2 and 3 (Skråppa 1996). Different correlation patterns were found for the selfed families in the three diallels, as was found here for the BLUP-predicted values of the parents. This may be due to population differences or be due to sampling effects caused by the relatively low number of parents from each population.

The nursery trials provide results of genetic variation in traits measured at a very early age which may not be related to adaptive or growth traits at later ages. They should not be used for the prediction of long-term performance of different families. Their importance will be studied in analyses of the relationships to traits measured in short-term trials and under long-term field conditions which will be presented by Skråppa et al. (2023) and Solvin et al. (in prep.).

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