Lammas shoots in Norway spruce families in short-term trials; genetic variation, inheritance patterns and implications of micro-environmental influence

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Abstract

This study presents information about the variability between and within populations of Norway spruce in lammas shoot formation. Assessments of lammas shoots were conducted in two short-term trials involving full sib families of Norway spruce from two complete diallel crosses, each originating from a natural population. These assessments were made over two growing seasons when the trees were six and seven years from seed, during which early summer temperatures varied significantly. The trees were grown on former agricultural land with large variation in soil fertility across the field. The proportion of trees with lammas shoots varied among blocks, ranging from 1 to 14 %, with the highest values in the blocks with the most fertile soil conditions. A substantial variation was also found among families from each population regarding the percentage of trees with lammas shoots, varying among half-sib families from 2 to 20 % and 1 to 19 % in the two populations, respectively. The largest part of this genetic variation was additive, with high values for the general combining ability (GCA) variance components and low values of the specific combining ability (SCA), maternal and reciprocal components. Estimates of narrow sense heritability were 0.40 for transformed lammas shoot scores in both diallels. Generally, families with an early start and early cessation of shoot elongation had the highest frequency of lammas shoots. In one of the diallels, families with a high lammas shoot percentage also had the highest number of ramicorn branches in a field trial at age 12 and 26 years from seed.

Key words: *Picea abies, diallels, lammas shoots, genetic variation, environmental factors.*

Introduction

The basic pattern of shoot growth in spruce species is predetermined growth, determined by the needle primordia in the overwintering terminal bud and their subsequent elongation in the next spring and early summer (Cannell and Johnstone 1978). The exception is the growth of the one-year-old seedlings which is solely based on the elongation of newly initiated needle primordia. This free growth will occur in diminishing proportions in subsequent years and will normally vanish before ten years after germination (Jablanczy 1971, von Wühlisch, Muhs 1986, Ununger et al. 1988). It can be distinguished from predetermined growth by changes in needle size, angle and needle internode length (Cannell, Johnstone 1978). A third mode of growth occurs when recently formed buds flush in late summer. This is called lammas growth, occurring after a second bud burst of the terminal bud the same growing season and with further shoot elongation (Kozlowski 1966). Bud burst of lateral buds on the leading shoot and subsequent elongation is called prolepsis. Here, the term lammas growth will be used to describe bud burst and /or elongation both from the terminal bud and from lateral buds of the leading shoot (von Wühlisch, Muhs 1986).

Lammas shoots often occur as a response to favourable environmental conditions for growth such as site fertility, soil moisture and nutrient availability (Kozlowski 1966, von Wühlisch, Muhs 1991). In Norway spruce, increasing occurrence of lammas shoots has been reported over the last years in Norway and in the Baltic region, possibly as an effect of changing climatic conditions. In a survey on forest land in lowland of South-East Norway it was found that lammas shoots are present with relatively high frequency on the most productive sites and that their occurrence increases the probability of development of multiple tops (forking) the following year (Kvaalen et al. 2010). This was confirmed by Granhus et al. (2019) who in two studies found that 57 % and 32 % of the sampled trees with multiple tops had signs of lammas growth. Lammas shoots may

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influence structural wood quality in a negative way and cause ramicorn branches and double whorls. Recent results from young Norway spruce plantations in Latvia show that the proportion of trees with lammas growth was highest on sites showing the most favourable micro-environmental conditions for spruce (Katrevics et al. 2018). In a study, conducted in two young (8–13 years) progeny tests established on fertile abandoned agricultural in Latvia, the proportion of trees with lammas shoots was highest among the tallest trees (47- 68 %) (Neimane et al. 2015). Thus, lammas shoots increased the length of annual height increment. In a recent study in young Norway spruce plantation in Lithuania, Danusevicius et al. (2024) found that trees with lammas growth were taller that those without lammas growth.

The formation of lammas shoots can delay the growth cessation, potentially postponing the onset of hardiness development, which could make the trees susceptible to frost injury during autumn. Additionally, late bud formation may affect the timing of bud burst in the following spring, thereby increasing the risk of spring frost injury, as it was observed by Skrøppa and Steffenrem (2016) in a progeny test. Such injuries to the terminal bud can result in two or more lateral branches competing for the lead.

Variation among Norway spruce provenances in the percentage of trees with lammas shoot was demonstrated at the end of growing season in a short-term trial on agricultural soil (Skrøppa et al. 1999). The northernmost provenances from Finland had the lowest value (18 %) while those from Poland considerably higher (82 %). Similar variation was observed by Danusevicius and Persson (1998) who found that provenances from Austria had the largest proportion of trees with lammas shoot and that there was a clinal variation among provenances from southern to northern Sweden. Clinal variation among provenances was also observed among provenances from an altitudinal transect from 600 to 1420 m in southern Poland (Skrøppa unpublished) and among provenances from a transect from 30 to 500 m in Central Norway (Skrøppa and Steffenrem 2019).

Few studies have characterized the variation in lammas shoots formation among and within natural populations of Norway spruce. Significant variation among families was observed within natural populations from Mid Norway (Skrøppa, Steffenrem 2019), and families with an early start and cessation of shoot growth were more prone to develop lammas shoots than those with later shoot development. In a study of epigenetic effects caused by temperature and daylength treatments during seed maturation, it was found that the treatments with the latest bud flush produced the tallest trees with the lowest frequencies of lammas shoots (Skrøppa 2022). Variation in lammas shoots frequencies among Norway spruce families from breeding populations was found in short-term trials by Hannerz et al. (1999) and Skrøppa and Steffenrem (2016). The last authors estimated a lower heritability value for families from Eastern European parents that had been selected after 25 years in a northern Swedish environment, compared to families from parents selected directly from natural Norwegian populations.

The main objectives with this paper were (1) to characterize patterns of variation in lammas shoot occurrence within natural populations of Norway spruce in short-term trials using full-sib families from complete diallels, and to illustrate possible implications for long term performance of these families in field trials, and (2) to demonstrate the effect of micro environmental conditions across a former agricultural field on lammas shoot occurrence.

Materials and methods

Two-year-old seedlings from full-sib families from three complete diallels, each made within a natural population of Norway spruce (Table 1), were planted in three trials at an agricultural field at Hogsmark Experimental Farm in the spring of 1976 (Skrøppa et al. 2023b). Each diallel trial was established with 48 trees from each full-sib family distributed in 4-tree square plots at a spacing of 0.6 m in 12 completely randomized blocks of size 164 m2. The diallels were of size 10 x 10 (Diallel 1 and Diallel 2) and 9 x 9 (Diallel 3) and with only few missing families. In each natural population, trees standing more than 50 m apart were randomly chosen among the trees having both female and male flowers and were crossed in all possible combinations. The short-term trials were located adjacent to one another with border rows of Norway spruce seedlings both between the trials and at the edges. The trials contained both selfed families, outcrossed full-sib families and open-pollinated half-sib families. Here results will be presented from the out-crossed full-sib families from Diallels 2 and 3, which showed high and variable proportion of trees with lammas growth. The two sets of families will be referred to as Diallel 2 and Diallel 3. The proportion of trees with lammas shoots in Diallel 1 were nearly zero, and the data were not included in further analysis.

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/ trial site	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

In nursery trials, terminal bud set was assessed at the end of the first growing season (Skrøppa et al. 2023a). In the short-term trials, measurements of tree heights were made at the end of growing seasons 7 and 10 years after seeding. Assessments were made of double leaders and ramicorn branches, and lengths of lammas shoots from the terminal bud longer than 2 cm were measured on all trees. During the sixth and seventh growing season (1979 and 1980), weekly shoot elongation measurements were taken in six blocks of each diallel. The start of shoot growth elongation (DAY1) and the cessation of shoot growth (DAY95; day of 95 % total leader growth) were estimated from the day count starting from April 1 (Skrøppa et al. 2023b). Assessments of free growth characteristics, continuous growth without bud formation, were also made. In September of same years, lammas growth on the terminal shoot was evaluated. Each tree in the three trials was scored in one of three classes (Figure 1):

1: No lammas growth on the terminal shoot, bud scales were closed.
2: The buds on the terminal shoot were swollen or had bud burst with an elongation less than 2 cm.
3: The buds on the terminal shoot had flushed and had an elongation longer than 2 cm.

(a) (b) (c)

Figure 1
Lammas shoot classes: Class 1 – Leader with bud scales closed (a); Class 2 – Bud scales are swollen but have not elongated; Class 3 – buds have flushed, and shoots have elongated. Photo: Gunnhild Søgaard, NIBIO.

The temperatures during the growing seasons 1979 and 1980 were quite different. April and May were colder than normal in 1979, whereas these two months were considerably warmer in 1980 (Table 2). The precipitation was high in June 1980

Table 2
Average monthly temperatures and precipitation for the growing seasons in 1979 and 1980 (Department of Physics and Meteorology, Agricultural University of Norway).

Month	1979		1980	
	Temperature °C	Precipitation mm	Temperature °C	Precipitation mm
April	3.4	65	5.5	10
May	8.0	88	11.7	60
June	15.3	41	15.7	136
July	15.2	55	16.2	47
August	13.7	85	14.8	75

One long-term field trial at a forest site was established with full-sib families from each half-diallel, planted with 4-tree plots in 12 blocks (Solvin et al. 2024). In these trials tree heights and diameters were measured up to age 32 years and damage scores were assessed stating whether the trees had ramicorns, double tops or double stems.

Calculations and statistical analyses

For each family, the percentage of trees with lammas shoots longer that 20 mm (class 3) was calculated, and family means were calculated over the two years with assessment. Similar mean values were also calculated for each block. The lammas shoot scores of each individual tree was transformed to normal scores within blocks and year by the Blom transformation in SAS (SAS Institute Inc. 2003). Pearson correlation coefficients were calculated between percentages and other traits.

Variance and covariance components for the transformed lammas shoot scores were estimated using the statistical package ASReml-R (Butler et al. 2017) by fitting the following linear model:

$$Y_{tijkl} = \mu + GCA_i + GCA_j + GCA_i \times Ye_{tis} + GCA_j \times Ya_t + RGCA_i - RGCA_j + SCA_{ij} + SCA_{ij} \times YEt_{ij} + \beta_{ij} \times RSCA_{ij} + \beta_{ij} \times RSCA_{ij} \times YEt_{ij} + P_{ijk} + IND_{ijkl} + E_{tijkl}$$

Here, Y_{tijkl} is a measurement in year t of an individual l in a 4-tree plot k in a cross between parents i and j, μ is the overall mean, GCA_i and GCA_j and $RGCA_i$ and $RGCA_j$ are random general combining abilities and reciprocal parent effects for i^{th} female and j^{th} male, respectively, $RGCA_i$ and $RGCA_j$ are the reciprocal parental or maternal effects, SCA_{ij} and $RSCA_{ij}$ are random specific combining abilities and reciprocal cross effects, respectively, for i^{ts} and j^{th} parents and β_{ij}= 1 for i<j, β_{ij}= - 1 for i>j. $GCA_i \times Ye_t$, $GCA_j \times YE_{tj}$, $SCA_{ij} \times YE_{tij}$, $\beta_{ij} \times RSCA_{ij} \times YE_{tij}$ are interaction effects with the year YE_t, P_{ijk} is the plot effect, IND_{ijkl} is effect of individual l in plot k, and E_{tijkl} is the error term. All factors and their interactions were fitted as random effects. Effects of year and block were not included due to the normal score transformation within each block and year.

In the ASReml analyses all effects were assumed to be random and to 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_E, 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 all the other variance component estimates to the estimate of σ^2_G. The narrow sense heritability was estimated as $h^2 = 4\sigma^2_{GCA}/\sigma^2_{phen}$. Significance of the variance components were indicated when the ratio of the variance components to its standard deviation (Z-test) was larger than 1.3 (Skrøppa et al. 2023b).

The ASReml analyses provide estimates of the different variance components and heritability. The standard errors of the estimates were calculated by first order Taylor series approximation by the ASReml-R software (Butler et al. 2017). The ASReml analyses also provided breeding values (BLUP) for the parents in each diallel. Pearson correlations were calculated between breeding values of traits to obtain proxy estimates of genetic correlations.

Results

Genetic variation and inheritance patterns

Results from the analyses of tree heights and the traits characterizing the timing of shoot elongation were published by Skrøppa et al. (2023b). Large within-population variation was shown for tree heights in all three diallels, and for the growth rhythm traits in Diallels 1 and 2, less in Diallel 3. GCA variance components were dominating for these traits. The mean day in 1979 for the initiation of shoot elongation (DAY1) was June 3 for the families in Diallels 2 and 3 and July 6 for shoot growth

A map of the blocks of the trials of Diallel 2 and Diallel 3 is shown in Figure 2. In the autumn of 1979 ten replicates of soil samples were collected in each of three rows across these blocks. Separate samples were collected in four depths between 5 and 50 cm. Chemical analyses were made of each sample and soil texture was analysed. Only minor differences were found in the chemical analyses of the soil samples across the block and soil depths. However, considerable differences were found in soil texture both among the three rows and in the depths of the organic layers, as summarized in Table 3. This indicates differences in soil fertility among the blocks, which may have implications for the growth conditions.

	G4 **XXXXX** 1.0 100	G9 **XXXXX** 6.7 105	B2 **XXXXX** 9.5 120	B7 **XXXXX** 6.8 105	
	G5 4.0 104	G10 9.1 116	B3 8.0 123	B8 6.7 121	B12 9.9 131
G1 **XXXXX** 7.1 117	G6 **XXXXX** 8.3 121	G11 **XXXXX** 9.0 114	B4 **XXXXX** 6.7 127	B9 **XXXXX** 12.0 127	
G2 13.2 138 **XXXXX**	G7 12.5 136 **XXXXX**	G12 13.4 134 **XXXXX**	B5 7.9 128 **XXXXX**	B10 8.0 123 **XXXXX**	
G3 14.1 132	G8 14.0 130	B1 8.3 133	B6 6.1 113	B11 6.9 113	

Figure 2
Map of the blocks of the trials for Diallel 2 and Diallel 3. The 12 blocks of Diallel 2 are noted by G1 to G12 and those of Diallel 3 by B1 to B12. The blocks had size 164 and 140 m2, respectively. XXXXX show the rows where soil samples were taken. Shown are also the mean percentage of trees with lammas shoot class 3 and mean tree height (cm) at the end of growing season seven.

Table 3
Characterization of soil samples. (Soil Survey Manual 1951. USDA Handbook No, 18, US Governmental Printing Office, Washington DC, 503 pp.)

Row of soil samples	Soil texture1)	Dept of organic layer
G4, G9, B2, B7	Silt loam 0 – 18 cm Silt clay loam 30 – 50 cm	20.6 cm
G1, G6, G11, B4, B9	Silt loam 0 – 30 cm Silt clay loam 30 – 50 cm	24.5 cm
G2, G7, G12, B5, B10	Silt loam 0 – 50 cm	26,7 cm

cessation (DAY95). For 1980, the corresponding days were May 27 and July 4. Thus, shoot elongation started seven days earlier in 1980 than in 1979, but the mean day of cessation of shoot growth was similar both years. Very few trees showed characteristics of free growth.

In Diallel 1, only 0.9 % of the trees were scored in class 3 in 1979. No assessment of lammas shoots were made in 1980. Analyses of lammas shoot records were not made for this diallel trial.

The mean percentages of trees scored in lammas shoot class 3 were 10.4 and 8.4 in Diallel 2 and 7.1 and 9.0 in Diallel 3, for the two years respectively. A large variation was observed between full-sib families in both diallels, as shown for the mean percentages of the two years in Tables 4 and 5. At the full-sib family level, high correlation coefficients were present between the family means of the two years, with r=0.88 and 0.80, respectively. Small differences were generally present between reciprocal crosses, and with few exceptions the means were equal for the same parent tree being used either as maternal or paternal parent. As examples, the families from crosses 11 x 17 and 17 x 11 had both 0 % trees with lammas shoots, and those from 14 x 20 and 20 x 14 had 40 and 34 %. In Diallel 3, parent 22 had offspring with very few lammas shoots, serving both as mother and father, and the offspring of parent 23 had high frequencies of lammas shoots.

Table 4
Mean percentage of trees with lammas shoots scored in class 3 for the years 1979 and 1980 in Diallel 2. Families after self-pollinations are deleted and five missing families are shown with -.

Father Mother	11	12	13	14	15	16	17	18	19	20	Mean
11		1	9	21	0	5	0	1	6	18	7
12	6		1	7	0	2	0	2	9	16	5
13	-	2		23	2	-	-	1	18	21	11
14	14	28	26		4	44	7	18	28	40	23
15	1	2	3	8		2	0	0	3	11	3
16	9	10	15	-	1		2	-	18	39	13
17	0	0	0	4	0	5		1	6	0	2
18	1	2	1	9	0	15	0		13	9	6
19	7	1	10	27	5	15	1	5		21	10
20	15	13	22	34	1	25	7	0	24		16
Mean	7	7	10	17	2	14	2	4	14	19	9

Table 5
Mean percentage of trees with lammas shoots scored in class 3 for the years 1979 and 1980 in Diallel 3. Families after self-pollinations are deleted and one missing family is shown with -.

Father Mother	21	22	23	24	25	26	27	28	29	Mean
21		0	26	9	9	3	8	11	12	10
22	1		1	3	2	1	0	0	0	1
23	40	3		27	14	5	14	20	12	17
24	15	1	40		7	1	7	6	17	12
25	7	0	18	10		2	4	9	1	6
26	3	0	17	0	2		10	3	0	5
27	8	1	20	4	-	0		4	14	8
28	14	2	27	11	8	0	2		9	9
29	5	0	16	9	3	0	3	7		5
Mean	12	1	21	9	6	2	6	7	8	8

In both diallels, the GCA variance component for the transformed lammas shoot score had the highest value of the genetic components and was highly significant (Table 6). The components of SCA were significant, but with low values. Some interactions with GCA and SCA and year were present, but also will low values. The estimates of heritability had the same value in the two diallels, with as high values as 0.40.

Table 6
Estimates of variance components and heritabilities for transformed lammas shoot score. Standard errors of estimates are presented in parentheses.

Sources of variation	Diallel 2	Diallel 3
GCA	0.062 (0.033)	0.064 (0.034)
GCA x year	0.010 (0.005)	0.002 (0.002)
RGCA	0 (0)	-
RGCA x year	0 (0)	-
SCA	0.006 (0.004)	0.014 (0.006).
SCA x year	0.006 (0.002)	0.004 (0.002)
RSCA	0 (0)	0.002 (0.002)
RSCA x year	0.001 (0.001)	0.002 (0.001)
Plot	0.029 (0.006)	0.036 (0.006)
IND	0.220 (0.009)	0.208 (0.009)
Error	0.255 (0.006)	0.271 (0.007)
Heritability	0.40 (0.17)	0.40 (0.17)

Variation among blocks

Considerable differences were present between blocks for the mean percentage of trees with lammas shoots (class 3) (Figure 2). This variation was largest in Diallel 2, with a range of variation from 1.0 to 14.1 %. The variation among blocks was lower in Diallel 3, with a range from 6.1 to 12.0 %. In Diallel 2, the correlation coefficient between the block percentage and mean tree heigh was as high as r=0.97, while it was r=0.49 in Diallel 3. This strong correlation in Diallel 2, could not be due to increased heights caused by tall lammas shoots, as the differences in block means were only slightly reduced when trees with lammas shoot score 3 were excluded.

In Diallel 2, there was a positive relationship at the block level between the timing of shoot growth cessation and percentage of trees with lammas growth (r=0.63 for DAY1 and r=0.90 for DAY95). The high values were in particular due to the low frequency of trees with lammas growth in blocks G4 and G5 (Figure 2) which had an early cessation of shoot growth and low tree heights. In Diallel 3, the mean lammas scores of the blocks were not significantly correlated to between-block variation in timing of the shoot growth period.

Trait relationships

The difference between the mean height of trees with and without lammas shoots (class 3 and class 1) was 18 and 17 cm in 1979 and 1980, respectively, in Diallel 2. The corresponding numbers in Diallel 3 were 15 and 10 cm. These differences were considerably larger than the mean lengths of the lammas shoots, showing that the group of trees with lammas shoots were generally taller also when the lengths of the lammas shoots are ignored. This is confirmed by the estimates of the positive genetic correlations between lammas shoot scores and tree height (Table 7).

Table 7
Estimated genetic correlations between transformed lammas shoot score and height, shoot growth start (DAY1) and cessation (DAY95) with standard errors in parentheses.

Trait	Diallel 2	Diallel 3
Height	0.37 (0.29)	0.69 (0.04)
DAY1	-0.72 (0.02)	-0.45 (0.22)
DAY95	-0.42 (0.22)	0.02 (0.95)

The strong negative correlation in Diallel 2 between the timing of shoot elongation (Table 7) is demonstrated in Figure 3, which presents the half-sib relationships between lammas shoot percentages and DAY1 and DAY95. Families with an early start and early cessation of shoot elongation generally had the highest frequency of lammas shoots. One exception was half-sib family 15 (Table 4, Figure 3) which had a low lammas shoot percentage and early initiation and cessation of shoot growth. In Diallel 3, these relationships were less clear (Figure 3). Here, the range of variation in the phenology traits, was smaller than in Diallel 2.

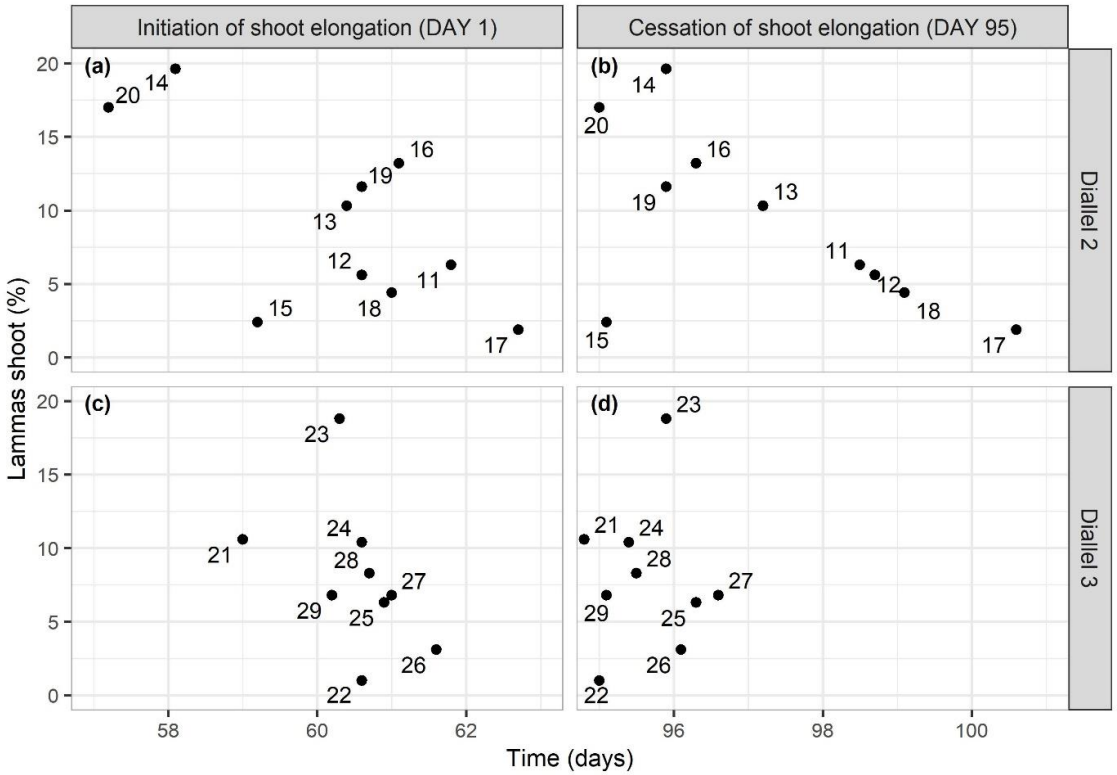

Figure 3
Comparative plots illustrating the percentage of lammas shoots against the day of initiation and cessation of shoot elongation. The data is presented for Diallel 2 (plots a and b) and Diallel 3 (plots c and d). Different half-sib families are distinguished by varying numbers.

In both diallels, less than 5 % of the trees produced double tops or ramicorn branches, with minor differences among half-sib families and no relationships with the percentage of trees with lammas growth.

In the field trial with full-sib families (half-diallel) from Diallel 2, there were positive relationships at the half-sib family level between percentage of ramicorn branches 12 and 26 years from seed and the lammas shoot percentage in the short-term trial with r=0.86 (p=0.001) and r=0.64 (p=0.05), respectively. No significant relationships were present for the percentages of double stems. A weak positive correlation was present between lammas shoot percentage and height after 26 years (r=0.24). In the field trial with families from Diallel 3, ramicorn branches and double stems occurred with low frequencies and no relationships were found with the lammas score percentages. The correlation coefficient between lammas shoot percentage and height after 32 years in this field trial was r=0.73 (p=0.02).

Discussion

This study presents information about variation in the occurrence of lammas shoots in progenies from a random set of parents from each of two natural Norway spruce populations. These progenies were planted in a former agricultural field to

which the populations were transferred from different altitudes. As the families were from controlled crosses made in a complete diallel design, inheritance patterns of lammas shoot performance can be characterized with estimates of genetic parameters. Such genetic information of within population variability of this trait has been presented in very few studies (e. g. Skrøppa et al. 1999, Skrøppa and Steffenrem 2019).

An important finding from this study was the large variation between the blocks in percentage of trees with lammas shoots. These differences were largest in Diallel 2 and were similar in both years. Each block of size 164 m^2 was planted with trees from the same families at a spacing of 0.6 m. The highest lammas shoot percentage was present in the blocks that had the most fertile soil conditions, indicated both by the soil analyses and the block mean tree heights. Although spring temperatures varied between the two years, leading to an early shoot growth initiation in 1980, the mean dates of shoot growth cessation were approximately the same. The high correlation coefficients between the block means of the two years indicate similar response both years. Thus, micro-environmental differences in soil fertility seem to be the most likely factor explaining the differences between blocks in both shoot growth phenology and lammas growth percentages. This corresponds with the results of Katrevics et al. (2018) and Danusevicius et al. (2024) from plantations of Norway spruce and von Wühlisch and Muhs (1991) in trials with provenances, and with those of Mørk (2023) who showed that application of nitrogen fertilizer increased the frequency of lammas growth.

The diallel families were transferred to a site with milder climatic conditions than at the site of their origins. The transfer was largest for the families in Diallel 1, from population Veldre (Diallel 1) at altitude 500 m with more severe climatic conditions than the two other populations (Table 1). Only a few trees in this diallel showed lammas growth. Populations transferred from high to low altitudes have earlier been shown to develop fewer lammas shoots compared to those from lower altitude (Skrøppa and Steffenrem 2017, 2019). The clinal variation, by latitude and altitude, demonstrated for provenances and populations, has been thought to be a photoperiodic response which is an indirect adaptation to the local temperature conditions (Ekberg et al. 1979). A similar photoperiodic effect, as for provenances, is most likely not present for families from the same population. Here, there was lack of relationship found between terminal bud set of these families the first growing season (Skrøppa et al. 2023a) and their lammas growth percentages.

No lammas shoots were observed in the three long-term field trials with the families from the half diallels. These trials were planted at forest sites with climatic conditions more like those of the original natural populations (Solvin et al. 2024). This shows that a high frequency of trees with lammas shoots after transfer to lower altitudes with better climatic conditions and to a more fertile site may not imply the same at forest sites.

The presented results demonstrate a large variation in lammas growth among families from the same natural population. The largest part of this variation was additive, with low values of SCA, maternal and reciprocal variance components. The heritability estimates, with the same size in both populations, were higher than that found by Skrøppa and Steffenrem (2019) in populations from more northern latitudes, but comparable to those found by Skrøppa and Steffenrem (2016) in a progeny test with families from breeding populations.

Families with an early start (Diallel 2 and 3) and early cessation (Diallel 2) of shoot growth have the highest frequency of lammas shoots. The same relationships with the phenology traits were present in Diallel 2 for the environmental influences at the block level. For Diallel 3 there was less variation among blocks both for the phenology traits and for height growth.

The strong additive genetic component to the variation suggests that tree breeding programs can reduce the frequencies of lammas flushing by recurrent selection by progeny testing, and seed production on selected parents in open-pollinated seed orchards. Furthermore, the relationships between the timing of shoot elongation start and cessation suggest that selection for late flushing material will give similar effect. Selection can be carried out at an early age in short-term tests and can easily be combined with selection for other traits, such as growth. Forest reproductive material from these seed orchards will be particularly beneficial for use on the most fertile sites. For the end-user, this selection may reduce the frequency of trees with ramicorn branches that reduce the strength and value of the wood.

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