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Variation among and within provenances of Norway spruce from Trøndelag and Nordland

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Divisjon for skog og utmark/Avdeling for skoggenetikk og biomangfold

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Variation among and within provenances of Norway spruce from Trøndelag and Nordland
Variasjon mellom og innen granprovenienser fra Trøndelag og Nordland

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Seedlings from seeds collected in three natural populations of Norway spruce (*Picea abies* (L. Karst)) in each of 21 provenances distributed between latitudes 63°N to 66°20'N and altitudes from 25 to 500 m in Trøndelag og Nordland counties were tested in nursery trials and one long-term field trial. Large provenance variation was found for phenology traits and early height growth in the nursery trials. A strong clinal variation was found for these traits relative to latitude and altitude. These relationships were weaker for height and diameter at ages 26 and 40 years. The timing of bud flush was strongly related to the temperature conditions at the seed collection sites, whilst terminal bud set and lammas shoot percentages showed high correlation coefficients with the provenance latitude. Provenances in the same geographic region showed large differences in height and diameter growth in the field trial. The long-term experimental site Spelrem is situated within the northern natural range of Norway spruce and the general trend in this material is that provenances from the northern part of the range perform better compared with provenances from more southern areas. Hence, the gain from provenance transfer seems to be limited under the present climatic conditions in this region.

Trær fra frø samlet inn i tre naturlige populasjoner av gran (*Picea abies* (L. Karst)) in hver av 21 provenienser mellom breddegradene 63°N til 66°20'N og høydelag fra 25 til 500 m i Trøndelag og Nordland ble testet i planteskoleforsøk og i ett feltforsøk. Det var i planteskoleforsøkene stor variasjon mellom provenienser for utviklingen av endeknopper om høsten og av knoppsprett om våren, frekvenser av trær med høstskudd og tidlig høydevekst. En sterk klinal variasjon ble funnet

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for disse egenskapene i forhold til proveniensenes breddegrad og høydag. Tilsvarende sammenhenger var svakere for høyde og diameter ved aldrene 26 og 40 år. Tidspunkt for knoppsett hadde sterk sammenheng med temperaturklimaet der frøet var sanket, mens knoppsetting og høstskudd viste sterkt sammenheng med proveniensens breddegrad. Provenienser fra samme geografiske område viste betydelige forskjeller for høyde og diameter i feltforsøket. Denne forsøkslokaliteten, Spelrem, ligger i den nordligste delen av det naturlige utbredelsesområdet til grana og resultatene herfra viser at trær fra provenienser fra dette nordlige området generelt vokser bedre enn de lengre sørfra. Det er derfor liten gevinst å hente ved å flytte provenienser nordover under dagens klimaforhold.

LAND/COUNTRY: Norge
FYLKE/COUNTY: Trøndelag og Nordland

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Preface

The Norwegian Forest Research Institute (Det norske Skogforsøksvesen) organized cone collections in Norway spruce stands in 21 municipalities in Sør- and Nord-Trøndelag and Nordland in 1970, a year with exceptional abundant spruce flowering in this region. The activities were initiated and lead by Jon Dietrichson and Per Brøndbo, with assistance from the local forest administration. Nursery trials were established at Skogstad and Stiklestad forest nurseries and early analyses of the measurements in the nurseries were initially made by Jon Dietrichson. Several colleagues have participated in the planting of a field trial and in measurements made in the trials. We would like to thank all persons that have participated in these activities, and in particular Jon Dietrichson, Per Brøndbo, Merete Larsmon, Gisle Skaret and Tove Skaret. Statistical analyses and the writing of the manuscript were done as part of the project “Klimatilpasset gran i Midt-Norge” that was financially supported by Allskog, Skogtiltaksfondet, Utviklingsfondet for skogbruket, Det norske Skogfrøverk and the European Union’s Horizon 2020 Research and Innovation Programme under grant agreement No 773383 (B4est). The institutions are thanked for their support.

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Arne Steffenrem

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1 Introduction

Norway spruce (*Picea abies* (L.) Karst.) has its extreme north-western distribution in the central and northern part of Norway. Based on pollen data and genetic data, the spruce populations became established approximately 3000 years ago in this region originating from a refugium located on the Russian plains (Giesecke & Bennet 2004; Latalowa & van der Knaap 2006, Tollefsrud et al. 2008). Recently, however, analyses of ancient DNA in lake sediments from north-western and Mid-Norway suggest that Norway spruce also was present at the Atlantic coast during the Last Glacial Maximum (17 700 year ago) and in the Trøndelag region 10 300 year ago (Parducci et al. 2012 a). The genetic variation in Norway spruce in the region is most likely influenced by this quite complicated evolutionary history in addition to the adaptive processes that have taken place, in particular related to the climatic conditions in the northern area.

During the last 30 years a number of studies have shown that Norway spruce in the boreal region can adjust its adaptive phenology by a rapid and most likely epigenetic mechanism, through a kind of a long-term memory of the climatic conditions during the seed maturation period (summarized in: Johnsen et al. 2009). Phenology and hardiness of progenies are influenced in a way such that seed production in a cold environment advances bud set and cold acclimation in the autumn as well as dehardening and flushing in the spring, whereas a warm reproductive environment delays the timing of these events. In a recent study, Solvin and Steffenrem (2019) have performed experiments with seedlings from Norway spruce provenances from seed lots produced in years with different temperatures. They show that seedlings from warm seed years had later bud flush, bud set and growth cessation. It has been suggested that these effects contribute, together with directional selection, to the steep clinal variation observed in adaptive traits in Norway spruce (Johnsen et al. 2009; Skrøppa et al. 2007).

A few provenance studies have provided information about variation in quantitative traits in Norway spruce provenances from Mid-Norway in comparison with provenances from more southern Norwegian origins or from the wide natural range of the species. Norway spruce provenances from Mid-Norway were included in two international IUFRO trials and showed high mortality and inferior growth when they were planted at more southern latitudes (Langlet 1960; Fottland and Skrøppa 1989; Persson and Persson 1992). Bergan (1994) showed clinal variation related to provenance latitude and altitude for phenology and growth traits in a series of trials at latitude 69 °N with provenances from the north-western region of Mid- and North-Norway. Clinal variation in the same traits was demonstrated by Skrøppa and Steffenrem (2019) for populations sampled along two altitudinal transects in Mid-Norway. Several studies with Norway spruce provenances from a wide latitudinal range in the Nordic countries (e. g. Dietrichson 1969; Krutzsch 1975; Dæhlen et al. 1995), and from altitudinal transects in Central Europe (e. g. Holzer 1993; Skrøppa and Magnussen 1993; Modrzyński 1995; Oleksyn et al. 1998), have shown clinal variation in adaptive traits with latitude and altitude. In Sweden, the clinal variation among provenances is stronger in the northern than in the southern part of the country (Danusevicius and Person 1998).

This study presents patterns of variation of phenology and growth traits within and among Norway spruce provenances from the northern geographic range in Norway, tested in the same region, and to compare these results with those of populations from a southern Norwegian provenance. It is based on measurements in nursery tests and in a long term field trial. The objectives were to characterize the clinal variation along transects based on latitude and altitude, and further provide information to guide the transfer of reproductive materials of local spruce provenances in the region and for the breeding programme for Norway spruce.

2 Materials and methods

2.1 Seed collection

In 1970, a year with abundant flowering in Norway spruce stands in the central and northern part of Norway; cones were collected from ten representative trees in each of three natural populations in 21 municipalities (provenances) in the counties Trøndelag and Nordland (Figure 1, Table 1). The three populations in each provenance were situated between 3 and 20 km apart and with less than 100 m difference in altitude. The overall mean range in latitude between provenances ranged from 63°N to 66°19'N and in altitude from 33 to 470 m. This range covered most of the natural distribution area of the species in this part of Norway and is geographically separated from the spruce regions further south (Figure 1). A similar collection was made the same year in three populations at Hurum, Buskerud, in southern Norway at latitude 59°37'N, altitude 90 -150 m. The ten seed lots from each stand were pooled into one population sample.

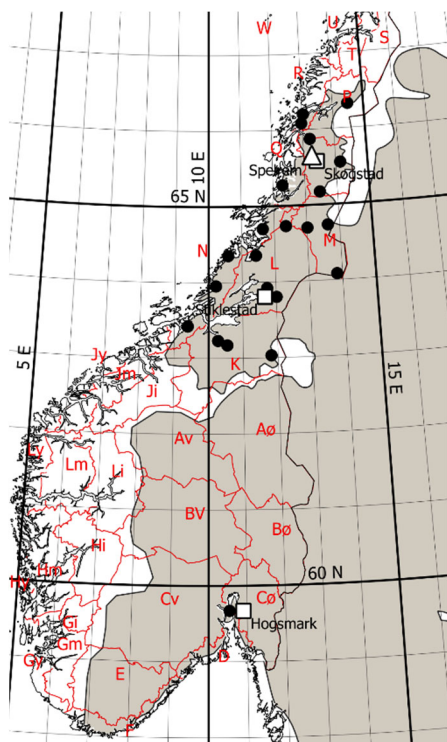


Figure 1. Localities in Trøndelag, Nordland and Buskerud where field collections of the tested populations were made (black dots), the nursery trials (open squares) and long-term trial in at Spelrem in Vefsn (open triangle). The western natural range for Norway spruce is shown as the shaded are and the red polygons show the seed zones defined by Skogfrøverket (Skogfrøverket 1995).

Daily mean temperatures for 1 x 1 km grid cells in Mid-Norway were obtained from the Norwegian Meteorological Institute (www.eklima.met.no) for long-term annual mean temperature for the reference period 1961-1990 and for the seed year 1970. Average temperature values for nearby grid cells with approximately same altitude as the actual populations where cones were collected were used to model temperature profiles for these locations, as described by Solvin and Steffenrem (2019). Two types of temperature parameters were generated for each provenance; annual mean temperatures for the period 1961 – 90 and mean temperatures for 1970 of the three months July, August and September, covering the seed maturation period. In addition, the mean temperatures for the spring months April, May and June were calculated. The long-term annual temperature means varied between 1.1 and 5.4°C for the 21 provenances, and the mean temperatures for the three months of 1970, varied from 10.6 to 12.6°C. Strong negative correlations were present between the mean temperature and the altitude of the provenances ($r=-0.83$), but not between mean temperature and latitude ($r=-0.21$).

Table 1. Mean values of provenances in the field trial at Spelrem. Seed collection zones are defined by Skogfrøverket (Skogfrøverket 1995).

Provenance/ Municipality	Seed collection zone	Latitude	Altitude M	Height age 40 cm	Diameter age 40 mm	Survival age 26 %	Damage age 40 %
Snillfjord	N1	63°25'	45	895	115	78	43
Åfjord	N1	63°57'	50	910	118	77	48
Klæbu/Melhus	K2	63°14'	175	907	117	70	40
Hølonda	K2	63°10'	208	937	120	76	52
Tydal	K5	63°02'	470	933	121	85	49
Steinkjer	L1	63°55'	103	892	117	83	45
Namsos	N1	64°21'	107	994	132	75	44
Verdal	L2	63°48'	160	959	126	82	40
Sørli	M3	64°05'	410	767	99	60	39
Røyrvik	M3	64°44'	382	831	106	87	42
Namsskogan	M1	64°42'	155	915	115	93	51
Høylandet	L1	64°44'	100	959	128	84	52
Fosnes	N1	64°42'	33	907	117	80	42
Flatanger	N1	64°21'	100	832	106	72	48
Bindal	Q1	65°16'	72	905	115	85	33
Leirfjord	P1	66°12'	87	872	109	87	46
Vefsn	O1	65°52'	70	855	109	90	54
Grane	O4	65°10'	382	743	90	76	43
Hattfjelldal	O3	65°33'	322	836	101	77	51
Korgen	P1	66°05'	132	971	125	82	47
Rana	P1	66°19'	120	855	110	92	49
Hurum	D1	59°40'	150	828	98	62	56

2.2 Nursery trials

The 66 seed samples were germinated in 1972 at two forest nurseries Skogstad, latitude 65°34'N (Nordland), and Stiklestad, latitude 63°47'N (Trøndelag). The germination was made in seed beds, and the seedlings were transplanted at the end of the second growth season in nursery experiments at both sites in four blocks with a varying number of seedlings per plot. Watering and fertilization were made according to standard nursery routines. Remnant seed lots from all seed lots were germinated in 1978 in the greenhouse at Hoxmark Experimental Farm at Ås, latitude 59°40'N, in multipot containers in four replicates.

The weights of 1000 filled seeds were determined for each seed lot. From the nursery trials, assessment and measurement data are available for the following sites and traits: bud flush at Skogstad at the beginning of the fourth growth season made the first week of June according to the Krutzsch scale (Krutzsch 1973); for height and classification of each seedling whether it had developed lammas shoots at the end of the fourth growth season at Stiklestad; and assessment of terminal bud set at the end of the first growth season at Hoxmark, defined as the percentage of seedlings with terminal bud. For lammas shoots and bud set the percentage of seedlings per plot that had the attained the characteristic was calculated. Higher values for bud flush and terminal bud set indicates early flushing and bud set, respectively.

2.3 Field trial in Nordland

Five-year-old seedlings from the 66 population seed samples were in 1977 planted in a long term field trial at Spelrem, Vefsn, at latitude 65°39'N and altitude 135 m, at spacing 2 m and in single tree plots with 20 replicates. The trial was thinned to approximately 55% of the originally planted trees 34 years after planting. Height growth has been regularly measured in this trial and assessments of occurred damage have been made. Here will be reported results for tree heights, survival and the frequency of double stems and spike knots ("stem damage") in 1997, 21 growth seasons after planting at age 26 years from seed, and height and diameter after thinning in 2011, 40 years from seed.

2.4 Field trials in Troms

Seedlings from the same material were planted in the period 1975-78 in trials at nine sites in Troms County at approximately latitude 69°N, altitude 70 -130 m. These trials were measured regularly up to 15-18 years after planting, and results for each individual trial were presented by Bergan (1994).

2.5 Statistical analyses

The statistical analyses were made of measurements from the nursery trials and the field trial in Nordland. Percentages per populations were calculated for mortality, occurrence of lammas shoots and damage. Assessment traits that occurred with a low frequency were not included in any statistical analyses. The bud flush assessments in classes were transformed to normal scores within blocks by the Blom method (PROC RANK, SAS Institute 2003) and the percentages by the square root arcsine transformation, and statistical analyses were made based on both the original observations and the transformed values. Only minor differences were found in these analyses of the untransformed and transformed observations.

Analyses of variance and regression analyses were made by the procedures GLM and REG in SAS (SAS Institute 2003). For seed weights and the nursery trial traits, arithmetic means were calculated for each population, and least square (LS) means were calculated for height and diameter in the field trial. Pearson correlation coefficients were calculated between provenance means. Linear regression analyses were made using the provenance mean as the dependent and the latitude, altitude and the

temperature parameters of the provenances as explanatory variables. The southern provenance, Hurum, was not included in the regression analyses.

Analyses of variance of the traits in the nursery trials were based on plot means, and the model included fixed effects of provenances and random effects of populations within provenances and blocks, in addition to the random error. Heights and diameter of individual trees in the field trial at Spelrem were analysed based on the same model. In these analyses the three populations from southern Norway were not included. For survival and top damage, differences among provenances were tested using variation among populations as error terms. Results from the analyses of variance and regression analyses are reported by p-values.

3 Results

3.1 Provenance variation

The range of variation among the mean 1000 seed weight of provenances was from 4.1 to 5.9 gram and significant variation was present both among provenances ($p < 0.0001$) and among populations within provenances ($p = 0.004$). There was a significant negative relationship between the seed weight and the altitude ($r = -0.59$, $p = 0.005$), but not between seed weight and latitude ($r = -0.36$, $p = 0.11$). The seed weight was positively related to the long-term mean temperatures ($r = 0.63$, $p = 0.002$) and also to the mean temperatures of the months July to September of the seed year 1970 ($r = 0.72$, $p = 0.0002$).

Highly significant variation was present among provenances for the four traits measured in the nursery trials (Table 2). The variation among populations within provenances was less, but was significant for terminal bud set, bud flush scores and lammas shoots. The seedlings from seed collected in the populations from the provenance in southern Norway were taller, had a later bud set and a higher frequency of lammas shoots than those from Mid-Norway.

Table 2. Range of variation for provenance means of the northern populations in the nursery trials for bud set, bud flush, lammas shoots and height, mean of the three southern populations, and p-values from the analyses of variance.

	Bud set	Bud flush	Lammas shoots	Height
	age 1	age 4	age 4	age 4
	%	scores	%	cm
Range of variation:				
northern provenances	58.0 - 98.8	2.2 – 2.8	10.2 – 55.2	15.9 – 20.7
Mean: southern provenance	10.9	2.4	82.1	22.4
Provenances	< 0.0001	< 0.0001	0.0001	0.0005
Populations (provenances)	< 0.0001	0.005	0.02	0.21

In the field trial at Spelrem, significant variation was present among provenances for height and diameter (Table 3), but less so among populations within provenances. For survival 21 years after planting, age 26 years from seed, the range of variation among provenances was from 70 to 93 % ($p = 0.01$), with the highest survival for the northernmost populations. The variation for stem damage, ranging from 33 to 54 %, was not significant. The three populations from southern Norway, not included in the analyses of variance, had the lowest survival and highest frequency of trees with damage.

Table 3. Range of variation for provenance means of the northern populations in the field trial at Spelrem for height and diameter, survival and damage, means of the three southern populations and p-values from the analyses of variance.

	Height age 26 m	Height age 40 m	Diameter age 40 cm	Survival age 26 %	Damage age 26 %
Range of variation:					
northern provenances	3.3 – 4.7	7.4 – 9.9	9.0 – 13.1	70.0 – 93.2	33.0 – 53.7
Mean: Southern provenance	3.6	8.3	9.8	61.7	56.0
p-values:					
Provenances	0.02	0.02	0.02	0.01	0.98
Populations (provenances)	0.17	0.05	0.06		

The provenances are located in seed collection zones (Skogfrøverket 1995) which again can be classified in larger provenance regions according to their prevailing climatic and geographic features. Three such regions and their corresponding seed collection zones are defined in Table 4 which also shows the means of each region for height, survival and damage in the trial at Spelrem. The means of the regions are quite similar. Within each region, however, the variation among provenances in height at age 40 years is quite large, with a range of variation from 8.3 to 9.9 m in the coastal region, and from 8.6 to 9.7 m in Nordland inland (Table 1).

Table 4. Means of traits in the Spelrem trial when the provenances are grouped in three geographic regions. The number of provenances in each region is denoted by n.

Geographic region	Seed collection Zones	n	Height age 40 m	Survival age 26 %	Damage age 26 %
Coastal <150 m	N1, Q1	6	9.1	79.9	43.0
Trøndelag inland <250 m	K2, L1, L2, M1	6	9.3	79.2	46.7
Nordland inland <150 m	O1, P1	4	8.9	87.5	49.0

3.2 Correlation patterns

The seed weight was negatively related to bud-set and flushing and positively to lammas shoots (Table 5). Quite strong relationships were also present among the phenology traits characterizing the annual growth rhythm (bud set, bud flush, and lammas shoots) at the provenance level, expressed by high absolute values of the correlation coefficients (Table 5). These traits were strongly correlated to the height at age four years. Their patterns of variation could to a large extent be explained by the combination of the geographic parameters latitude and altitude and of temperature sums of the provenances as shown in Table 6. The timing of bud set and frequencies lammas growth are strongly related to the latitude of the provenances and less to the temperatures. The most northern provenances have an early bud set and a lower frequency of trees with lammas growth. The timing of bud flush is much more related to the temperature conditions. A calculation of the long term mean temperatures of the spring months April, May and June for each provenance showed a correlation coefficient between this mean and the mean flushing score of $r = -0.87$.

Table 5. Pearson correlation coefficients between provenance means of traits in the nursery trials and in the field trial. Absolute values higher than 0.55 are significant at the 1 % level. Higher values for bud flush and bud set indicates early flushing and bud set, respectively.

	Bud set age 1	Bud flush age 4	Lammas growth age 4	Height age 4	Height age 26	Height age 40	Diameter age 40	Survival age 26
Seed weight	- 0.50	- 0.75	0.75	0.76	0.58	0.51	0.40	0.22
Bud set		0.61	- 0.83	- 0.62	- 0.29	- 0.46	- 0.48	0.40
Bud flush			- 0.75	- 0.80	- 0.49	- 0.59	- 0.60	- 0.03
Lammas growth				0.77	0.29	0.48	0.53	- 0.40
Height age 4					0.56	0.63	0.66	- 0.10
Height age 26						0.82	0.79	0.52
Height age 40							0.98	0.25
Diameter age 40								0.18

Table 6. Pearson correlation coefficients between provenance means of the northern populations of traits in the nursery trials and latitude, altitude and temperature profiles of the provenances. Absolute values higher than 0.55 are significant at the 1 % level.

	Annual mean temperature 1961-90	Mean temperature July – September 1970	Latitude	Altitude
Bud set	- 0.40	- 0.21	0.88	0.03
Bud flush	- 0.77	- 0.79	0.41	0.67
Lammas shoots	0.59	0.44	- 0.88	- 0.27
Height	0.59	0.67	- 0.51	- 0.53

The results from the multiple regression analyses presented in Table 7, with both latitude and altitude as explanatory variables, and illustrated in Fig. 2, show that the more northern or high altitude provenances had the earliest initiation of growth, the earliest bud set and the lowest frequency of lammas shoots. It is remarkable that latitude and altitude explained as much as 94 and 80 % of the variation among provenances for lammas shoots and bud set, respectively. Height and diameter growth in the long term field trial were to some extent statistically related to the growth rhythm traits, in particular to the timing of flushing. However, latitude and altitude could to a lesser degree explain the variability in the growth traits, as shown by the lower values of the coefficient of determination (Table 7).

Table 7. Estimated regression coefficients for latitude and altitude, their p-values in the full model in parenthesis and the coefficient of determination R^2 in regression analyses of provenance means of the provenances from Trøndelag and Nordland. Bud flush has units on the Krutzsch scale.

Trait; unit	Latitude	Altitude	R^2
Bud set age 1; %	11.60 (<0.001)	0.02 (0.07)	0.81
Bud flush age 4; scale	0.09 (<0.001)	0.0009 (<0.001)	0.74
Lammas growth age 4; %	- 14.25 (<0.001)	- 0.05 (<0.001)	0.94
Height age 4; cm	- 0.72 (<0.001)	- 0.006 (<0.001)	0.66
Height age 26; cm	- 6.30 (0.33)	- 0.073 (0.03)	0.16
Height age 40; cm	- 22.64 (0.07)	- 0.19 (0.08)	0.28
Diameter age 40; cm	- 4.014 (0.04)	- 0.004 (0.05)	0.33

In the regression analyses made to study the relationships between the same traits and the long term annual mean temperatures and the means of the months of July to September of the seed year 1970, weaker relationships were found than those based on latitude and altitude, as presented in Table 7.

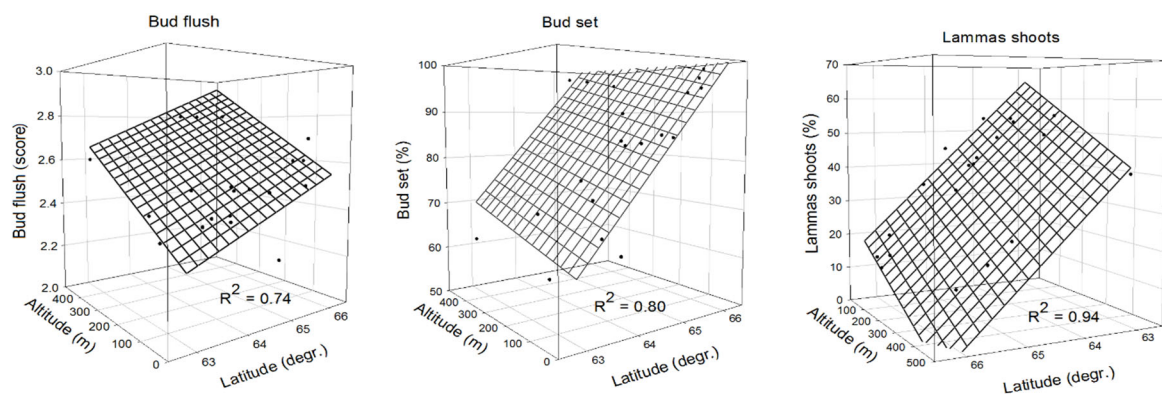


Figure 2. Illustration of the regression models with latitude and altitude as explanatory variables and bud flush, bud set and lammas shoots as the dependent variable, respectively.

4 Discussion and conclusions

The Norway spruce provenances tested in this study cover the whole natural range of the species in the Norway north of latitude 63°N and in an altitudinal range from 30 to 500 m. A striking result is the strong relationship observed between the latitude and altitude of provenances and the phenology traits measured in the nursery. The two geographic parameters explain between 74 and 95 % of the variability in the regression analyses of the phenology traits measured at the nursery stage (Table 6, Figure 2). Taking the quite narrow range in latitude into account, this is a surprisingly high level of determination. Some variation is present among closely located populations within municipalities, but to a much smaller extent.

The clinal variation patterns found here related to latitude and altitude corresponds to what have been found in earlier provenance studies with Norway spruce (e. g. Dietrichson 1969; Krutzsch 1975; Holzer 1993; Skrøppa and Magnussen 1993; Dæhlen et al. 1995; Modrzynski 1995; Oleksyn et al. 1998). The provenances in those studies, however, cover a much wider geographic range. Clinal variation in phenology traits was also found for Norway spruce populations along two altitudinal transects in Trøndelag in a recent study by Skrøppa and Steffenrem (2019).

It has been assumed that long-term adaptation to the climatic conditions has played a major role for the observed clinal variation patterns found for phenology traits such as bud burst in the spring and growth cessation and bud set in the autumn (Eriksson et al. 2013). It may be advantageous for northern and high altitude populations to respond rapidly to high temperatures in the spring and likewise react to short night lengths and lower temperatures before the end of the summer for building up hardiness. However, another contributing factor to the observed clinal variation may be the epigenetic memory effect of temperature conditions during seed maturation that in particular influences phenology traits of Norway spruce seedlings and young trees (Johnsen et al. 2009). High temperatures during seed maturation imply delayed phenology and lower temperatures the opposite. Recent results from trials with Norway spruce provenances from seed lots collected in Mid-Norway in years with different climatic conditions confirm that such an epigenetic memory effect is an important component of the clinal patterns found in phenology traits (Solvin & Steffenrem 2019). In our study, all seed lots were collected in the same year, and quite high values were found for the correlation coefficients between provenance means of the phenology traits and both the mean temperature during the seed maturation period and the long term annual mean temperature. It is therefore not possible with our data to separate between influences of long-term genetic adaptation to temperature conditions and epigenetic effects of temperatures the specific seed year.

Seedling height at age four years was strongly related to the phenology traits and showed similar clinal variation patterns. In the field trial, negative relationships were present between height and diameter and the geographic parameters of the provenances, indicating better growth of the more southern and low altitude provenances. However, the clinal patterns of variation were expressed to a much less extent for the late growth traits than for the phenology traits measured at an early age. Provenances with good height growth were found in each of the three geographic regions. Those with inferior growth were from the highest altitudes. The more northern provenances generally had the best survival.

Bud set and lammas shoot percentages were strongly related to provenance latitude and less to the temperature conditions, with an early bud set and low level lammas shoots for the northern provenance. The timing of bud flush, on the other hand, showed stronger relationships to the temperature conditions. These patterns correspond with what is known of the environmental triggers of these traits; the timing bud burst is strongly related to spring temperatures in spring (e. g. Hannerz 1999), whereas bud set takes place by a photoperiodic response that show provenance variation with

latitude (Dormling 1973). Environmental and genetic factors related to lammas growth formation are less known, see discussion in Skrøppa and Steffenrem (2017, 2019).

Bergan (1994) presented results with the same material planted at nine sites at latitude 69°N in Troms County. He found high correlations between the mean heights and the latitude of the provenances; with decreasing heights from north to south. The provenances differences in height were not significant at localities with low frost risk. In these trials the frost damage increased from northern to the southern provenances. The results from the trial at Spelrem correspond quite well with those reported by Bergan (1994). The climatic conditions at this site are less severe than those at most of the sites in Troms.

Some variation was present among populations within provenances for bud set, bud flush and lammas shoots, but not for height age 4 years and height and diameter at later ages. The variation among populations found here was smaller than the variation among closely related populations in the same provenances of Norway spruce at high altitudes in southern Norway reported by Dietrichson (1973) for traits measured in the nursery.

The seedlings from the three populations of the provenance from latitude 59°40'N in southern Norway had a later terminal bud set, and a higher frequency of lammas shoots and were taller at age four years than the seedlings from northern populations. In the field trial, however, growth was not superior and the survival percentage was low. This was similar to the results from Troms (Bergan 1994), where this provenance had a low survival percentage. Seedlings from populations close to latitude 60°N in southern Norway are certainly not well adapted to the northern environment.

Recommendations for the use of provenances should be based on both short term trials and field trials planted at several sites. Only one field trial is represented in this study. At Spelrem both northern and southern provenances from Midt-Norway showed satisfying growth and survival. The local climatic conditions at this site are most likely representative for an average site in the region, and in contrast to other studies of Norway spruce (e.g. Rosvall and Ericsson 1982), this study shows no positive effects of provenance transfer from southern latitudes or from lower elevations. This might, however, change under climate change conditions as the increase in temperatures are expected to be significant in the north.

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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.