NDH: One zone of the MNR zymograms with lowest migration rate proved to be another enzyme system, NDH. The reason for this conclusion is that this zone also appears when the gel is stained for NADH dehydrogenase. The NDH zone was found to reveal 6 variants of which 3 were single-band and 3 were multi-band phenotypes. Since the multi-band phenotypes consisted of 3 individual bands, it is assumed that this zone belongs to a dimeric enzyme.

PGM: This enzyme pattern consists of 3 zones. Variation could be found in 2 of these zones. The fastest migrating zone (PGM-A) shows in total 6 isoenzyme variants, 3 single-band and 3 double-band variants which were assumed to be heterozygous phenotypes, as this enzyme system is generally monomeric. The slowest migrating zone (PGM-C) appears to have 3 isoenzyme variants, 2 single-band and 1 double-band phenotypes, which again was regarded as the heterozygous expression of this monomeric enzyme.

MDH: This enzyme system shows 3 activity zones in zymograms, but only the intermediate zone (MDH-B) was found to exhibit variation. Two variants appear in this zone, a single-band variant and a triple-band variant, which was assumed to be the heterozygous phenotype of this dimeric enzyme system. A second single-band variant expressed by the other homozygous phenotype was not detected in our material.

3.2 Results of the genetic analysis and discussion

For each individual with a putative heterozygous seed perisperm isoenzyme pattern, a number of seed embryos (offspring genotypes) were analyzed. *Table 1* shows these individuals, grouped according to proposed heterozygous phenotype, together with the corresponding phenotypes of their progenies. The quantitative relations (ii) and, where possible, (iii) were tested using the exact binomial goodness-of-fit test, the exact levels of significance being given in *table 1*.

For all variable isoenzyme zones, the qualitative and quantitative conditions for a codominant mode of inheritance at single loci are fulfilled. Each offspring possesses at least one maternal allele, and none of the progeny phenotypic structures shows significant deviation from the ratios expected under equations (ii) and (iii). Equation (ii) was tested in all combinations of alleles recovered at a gene locus. Therefore, in all cases there is no apparent reason to reject the hypothesis of a single-locus, codominant mode of inheritance.

The conditions in cypress seed described in section 2.1 eliminate the necessity of sampling either buds or several endosperms for genotyping seed trees. The diploid genotype of the seed parent is expressed in the active seed perisperm, which can be assayed in 1 seed.

Acknowledgements

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Provenance Variation in Shoot Growth Components of Norway Spruce

By T. Skrøppa[1]) and S. Magnussen[2])

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Abstract

The elongation of terminal shoots was measured during 2 growth seasons in a Norway spruce (*Picea abies* (L.) Karst.) provenance trial, comprising 36 provenances. Significant variation was found between provenance regions for traits that characterize the timing and duration of the growth period, but not for the rate of growth. Provenances from the Nordic countries terminated their growth 20 days earlier in the summer than the provenances from Eastern Poland which had the latest growth cessation. The duration of the growth period accounted for the larger part of the variation in shoot growth (80%) among provenances, while the rate of growth was an equally important factor within provenances. The day of growth cessation, the duration of the growth period and total annual shoot growth were closely correlated to altitude for provenances originating along an altitudinal gradient, but no such correlation was found between rate of growth and altitude. Within a provenance region in southern Poland the variation among provenances was exclusively in the timing and duration of the growth period. In another region in the Baltic countries, variation in the rate of growth was equally important as its duration for determining total shoot growth.

Key words: Picea abies, provenances, shoot growth components, adaptation.

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[1]) Norwegian Forest Research Institute, 1432 As, Norway

[2]) Petawawa National Forestry Institute, Forestry Canada, Chalk River, Ontario, Canada K0J 1J0

Introduction

The shoot growth of conifers in the temperate zone is a 2-year process which starts with the bud formation the first year and continues with the extension of the shoot the second year (Kozlowski, 1964). Three main factors characterize the yearly pattern of shoot extension: the flushing or shoot initiation in the spring or early summer, the elongation of the shoot during a relatively short period in the summer, and the cessation of growth and bud formation. All processes are initiated and controlled by environmental factors. However, a considerable genetic variation in response has been shown both at the species, provenance and individual tree level (Kozlowski, 1964). Inherent variability is present for the time of flushing, the duration of the growth period and the intensity of growth (Cannell et al., 1976) and for growth cessation (Ekberg et al., 1976). At the provenance level this variability can in many cases be considered as a direct adaption to the environment (Ekberg et al., 1976).

Provenances of Norway spruce (*Picea abies* (L.) Karst.) have been shown to differ considerably both in their timing of flushing (e. g. Langlet, 1960; Krutzsch, 1975) and in growth cessation (e. g. Dormling, 1973). Generally, the most northern provenances will have the earliest shoot growth initiation, while the provenances from the continental parts of East Europe will be the latest (Langlet, 1960). The northern provenances or those from high altitudes will have the earliest cessation of growth (Dormling, 1973; Holzer, 1978). Substantial differences in height growth have been found between provenances (e. g. Giertych, 1976; König, 1981; Fottland and Skrøppa, 1989). Under favourable climatic conditions in the Scandinavian countries, provenances that are transferred from Central and Eastern Europe will grow better than the local sources (Langlet, 1960; Fottland and Skrøppa, 1989). This can be due to a longer growth period, a faster growth rate or a combination of both.

This report presents the results of a 2-year study of the annual shoot growth pattern in a Norway spruce provenance trial. The objectives of this work were: (i) to separate the annual shoot growth into the 2 components, length of the elongation period and intensity of growth, (ii) to study provenance differences in the 2 shoot growth components, and (iii) to determine the relative importance of the 2 components for determining annual shoot growth at the provenance level. Such information is important for interpreting provenance differences in height growth and understanding their relationships to climatic adaptation. It is also important for a proper selection of provenances for commercial planting and of genotypes to be included in the breeding populations.

Figure 1. — Geographic origins of the provenances included in the experiment. The 6 zones are indicated by the zone number and border lines.

Table 1. — Geographic zones comprising 25 provenances in the trial. Minimum and maximum value of the geographic parameters are shown in upper line and lower line, respectively.

Zone	Description	Range in geographic parameters			Number of provenences
		latitude	longitude	altitude	
1	Nordic countries	57°32' 60°03'	8°44' 23°06'	15 250	3
2	Latvia	56°27' 57°29'	21°35' 25°55'	45 210	8
3	North eastern Poland	53°41' 54°10'	20°34' 23°03'	160 180	4
4	Eastern Poland	50°34' 51°04'	20°41' 22°58'	260 310	2
5	Southern Poland	49°29' 49°40'	18°40' 19°01'	600 800	5
6	Czechoslovakia	48°44' 49°05'	19°44' 22°52'	700 750	3

Materials and Methods

Provenances

This study comprised seedlots from 36 different geographic origins or provenances of Norway spruce. Each lot represented one stand and was in most cases collected from more than 20 trees. The origins of the 36 provenances are shown on the map in *Figure 1.* Twenty were from Poland, 8 from Latvia, 3 from Czechoslovakia, and 1 provenance originated from each of the countries Romania, Germany, Finland, Sweden and Norway. Twenty-five of the provenances can be grouped into the 6 more or less homogenous geographic zones shown in *table 1*, see also *figure 1.* The zones were used to study the variation among provenances within smaller geographic regions in comparison with the more large scale variation among the zones.

Three provenances came from the same geographic region as the 5 provenances in Zone 5 (South Poland), but from higher altitudes (950m, 1050m and 1450m). This set of eight provenances was used to study the variation among stands from different altitudes within the same geographic region.

Experiment

Measurements

A short term experiment was planted at Ås, Norway, in the spring of 1976 with 2-year old seedlings. The experimental design was randomized blocks in 4-tree square plots and 16 replicates. The experiment was planted at cultivated soils at 0.6m spacing.

In the sixth (1979) and seventh (1980) growth season weekly measurements were made of the elongation of the terminal shoot. All trees were measured in 6 replicates in 1979 and in 8 replicates in 1980. The measurements were made in millimeters from a fixed base point to the tip of the shoot. In 1979, the dates of measurement were June 7, 13, 20, 28 and July 3, 12 and 23, with a final measurement on August 17. The next year, measurements were made on May 27, June 2, 9, 16, 23, 30, July 4, 10, 18, 25 and August 26. The elongation from a second flush after the termination of normal growth (lammas growth) was not included in the measurements.

The relative proportion of unlignified wood in the current annual ring on September 10, 1980, was determined on the 4 trees in 6 replicates from each of 10 provenances. Wood samples were then collected, and the percentage of unlignified wood was later determined (Dietrichson, 1964; method III). The degree of lignification provides a measure of growth cessation in the wood.

Measurements of tree heights were made regularly in the experiment, with a final measurement when it was terminated in 1982, at age 9 years from seed.

Sixteen of the same provenances were included in a provenance trial in West-Norway (Magnesen, pers. com.). Here assessments were made of bud-set after one growth season in the nursery on October 9, 1974, and heights were measured in the field test at 13 years from seed in 1986.

Statistical methods

The elongation at each day of measurement was calculated in percentage of final shoot length for each individual tree. Weibull distribution functions were fitted to each plot based on the relative elongation measurements of the 4 trees on the plot. With this function, the relative elongation at day x can be described by

F (x) = 1 — exp (—((x — a) / b) ** c)

where

a is the earliest day of growth initiation,
b is a scale parameter,
c is a shape parameter.

In the estimation procedure, April 1 was arbitrary set equal to day 1. Individual estimates of a, b and c were found for each plot and year, a total of 503 plots, by the nonlinear estimation procedure PROC NLIN in Statistical Analysis System (SAS) (SAS Institute, 1987).

The goodness of fit of the estimated functions was tested by the Kolmogorov-Smirnov test (Fitz, 1963). Since each curve was fitted to the measurements made on the individual trees of 4-tree plots, 4 replicated observations were available at each date. This made it possible to partition the residual sum of squares into 2 components, 1 component measuring the variation among the 4 observations at each date, and the other the deviations of their mean values from the fitted curve. Thus, the lack of fit could be tested by an F-ratio test. It is approximate due to the non-linear estimation procedure (Gallant, 1987).

From each estimated Weibull curve the following characteristics were calculated:

DAY1 = day of completion of first 20 mm elongation (growth start day)
DAY2 = day when last 20mm of total elongation still is to be completed (growth cessation day)
DAYS = DAY2 — DAY1 (length of the elongation period)
RSE = average rate of shoot elongation (mm/day) during period between DAY1 and DAY2.

DAY1 and DAY2 will be used to describe growth start and growth cessation, respectively, and DAYS to measure the length of the elongation period. RSE characterizes the average rate of shoot elongation, i. e. the predominantly linear part of the Weibull curve.

Analyses of variance were performed for the 4 elongation characteristics and for annual shoot length (ASL). All analyses were based on plot values. Two separate ANOVAs were performed, all with the procedure PROC GLM in SAS. The first included all 36 provenances following the model

$$Y_{jtk} = \mu + A_t + P_j + (AP)_{tj} + R_k + (AR)_{tk} + E_{tjk} \qquad (1)$$

where

Y_{tjk} is the plot mean value of provenance j in year t, μ is a constant, A_t and P_j are the year and provenance main effects, respectively, $(AP)_{tj}$ is their interaction, R_k is the block effect, $(AR)_{tk}$ is the interaction with year and block and E_{tjk} is the residual error. All effects, except μ, are considered as random.

A second analysis was performed for the 26 provenances pooled into Zones 1 to 6 (*Table 1*). Here, the zone effect, Z_i, was considered as fixed and the provenances within zones as random. This gives the model

$$Y_{tijk} = \mu + A_t + Z_j + P_{ij} + (AZ)_{ti} + (AP)_{tij} + R_k + (AR)_{tk} + E_{tijk} \qquad (2)$$

Bonferroni t-tests at 5% level were used in multiple comparisons between zone means (Miller, 1981).

A similar ANOVA was performed for the unlignified proportions of the annual ring in 1979 based on individual tree values of the 4 trees in each of 6 replicates.

The 9 provenances in the altitudinal transect study were subject to separate regression analyses, based on provenance mean values in each year. The model for this analysis was

$$Y_{tj} = \mu + a_t + b_tH_j + E_{tj} \qquad (3)$$

where

H_j is the altitude of provenance j, b_t is a regression coefficient that can be different for the two years and E_{tj} is the residual error.

Correlation coefficients were calculated between the shoot elongation parameters and between these variables and annual shoot lengths, tree heights and percentages of lignification and terminal bud-set.

The relative influence of the length of the elongation period (DAYS) and the rate of shoot elongation (RSE) on annual shoot lenght (ASL) can be studied by path coefficient analyses (KREMER and LARSON, 1983; MAGNUSSEN and YEATMAN, 1989). On the basis of the relationship log (ASL) = log(DAYS) + log(RSE), the relative contributions of the two factors can be expressed by the products of their respective path coefficient and correlation coefficient to log(ASL) (MAGNUSSEN and YEATMAN, 1989). This product, called the degree of determination, was calculated both between provenances and between plots within provenances from the estimated variance-covariance matrices in a multivariate analysis of variance of the three variables log(ASL), log(DAYS) and log (RSE), with provenances and replicates as factors.

Results

Estimation of Weibull functions

The WEIBULL distribution curves gave a satisfactory fit to the observed cumulative shoot elongation measurements. The KOLMOGOROV-SMIRNOV test showed significant deviations on none of the 503 plots, while the ratio of mean squares for testing the appropriateness of the model exceeded the 5% level critical value of the F-test only in 7 plots. Examples of the fit of growth curves to individual plots are shown in *figure 2*, where WEIBULL functions are fitted to the same 2 provenances in 2 replicates.

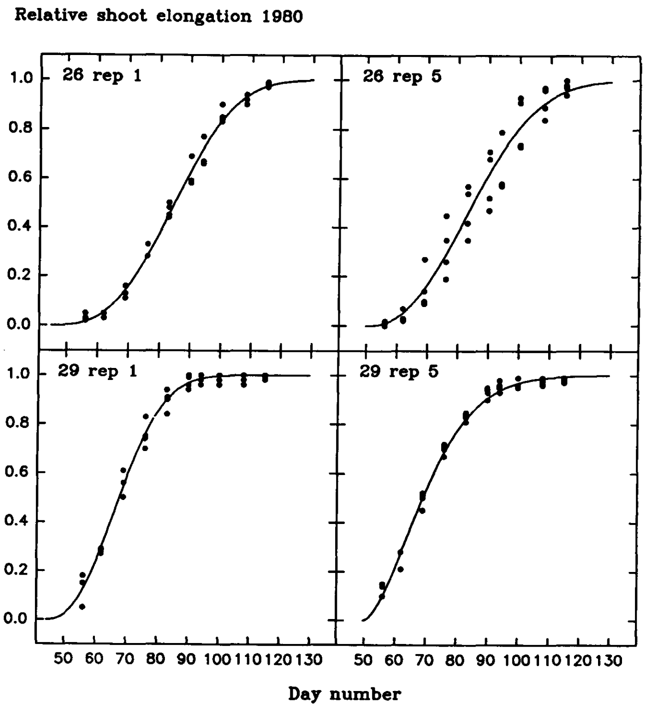

Figure 2. — Relative shoot elongation curves in 2 replicates for the provenances: Lubelski, Poland (#26 top), and Solbøle, Finland (#29 bottom).

Variation in shoot growth

In the spring of 1979, when the measurements started, the mean tree height was 53 centimeter (cm), and the range of variation between provenance means was from 42 cm to 58 cm. In 1979, the mean shoot growth was 33 cm, and in 1980 55 cm. The variation between provenance means was from 25 cm to 41 cm and from 47 cm to 65 cm in the 2 years, respectively. This variation was highly significant in the analysis of variance based on model (1) (*Table 2*). Significant variation for ASL also occurred between years and between replicates, but the interactions between provenance and year, and between year and replicate were not significant ($p > 0.05$).

Table 2. — Results from analyses of variance based on model (1). The table shows p-values of F-tests.

Source	ASL	DAY1	DAY2	DAYS	RSE
Provenance	<0.0001	<0.0001	<0.0001	<0.0001	0.04
Year	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Provenance x year	0.92	0.86	0.91	0.94	0.37
Replicate	<0.0001	0.0018	0.001	0.01	0.0002
Year x replicate	0.93	0.0001	0.98	0.75	0.94

ASL : annual shoot length
DAY1 : growth start day
DAY2 : growth cessation day
DAYS: duration of the shoot elongation period
RSE : rate of shoot elongation

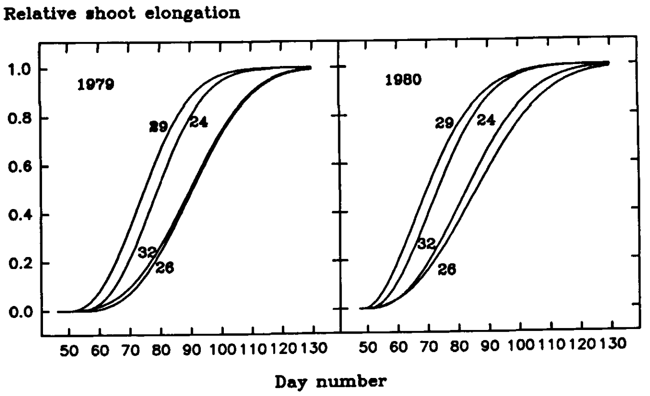

Figure 3. — Relative mean shoot elongation curves in 1979 and 1980 for the four provenances: Witow, Poland (#24), Solbøle, Finland (#29), Lubelski, Poland (#26), and Doria Cindreni, Romania (#32).

Timing of shoot elongation

At the first shoot growth measurement in 1979, on June 7, the elongation had started in all provenances, but the percentage of elongation completed varied from 3% to 25% at the provenance mean level. Similarly, on the first day of measurement in 1980, the provenance means varied from 2% to 12%. The Finnish provenance Solbøle (#29) initiated in both years shoot growth earlier than any other provenance. Its growth started 11 days (1979) and 10 days (1980) earlier than the latest provenance, Lubelski, East Poland (#26). At the end of the elongation period, 6 to 8 weeks later, a similar, but extended variation was observed in growth cessation. The mean difference in DAY2 between the 2 provenances (#29 and #26) was 19 days in 1979 and 21 days in 1980. The difference in the length of the elongation period (DAYS) was 10 days both years, with the longest shoot elongation period for the most southern provenance. The mean elongation curves of 4 provenances are shown in *figure 3* for 1979 and 1980 separately. The provenances #24 and #29 have a rather short elongation period with an early cessation of growth, while provenances #26 and #32 extend their growth later in the summer.

Table 2 presents a summary of the ANOVA results from the model (1) analyses for the shoot growth characteristics. For all variables the variation among provenances was highly significant. The 2 years, 1979 and 1980, also differed, but no interactions were found between provenances and years. The significant year x replicate interaction for DAY1 was caused by 3 adjacent replicates that initiated shoot growth on an average 2 days earlier than the other replicates in 1980, while they were not different in 1979.

Zonal effects

The between-provenance variation is a mixture of differences between stands in the same geographic region and stands in separated regions. The analyses of variance based on model (2) take this into account, considering the zones as fixed, and the provenances within zones as random. For the variables characterizing the initiation (DAY1), the cessation (DAY2) and the duration of the shoot elongation period (DAYS), there was a considerable and significant variation between zones (*Table 3*). The variation among provenances within zones was significant for all characters. No interaction effects were present.

The means of the zones averaged over both years, the range of variation within zones (min and max) and the conclusions from the multiple comparison tests are shown in *figure 4*. The mean shoot elongation period of Zone 1 was different from the other zones with an earlier growth initiation and cessation and a shorter elongation period, as shown by the variables DAY1, DAY2 and DAYS. Note that the difference between Zone 1 and Zone 5 was not significant for DAY1, neither was the difference between Zone 1 and Zone 2 for DAYS. Provenances in Zones 3 and 4 were generally the last to start the shoot growth and were also the last to terminate growth. Three zones with the highest annual shoot lengths (Zones 4, 5 and 6) also had the longest elongation periods. The only Romanian provenance included in the study, Dorna Cindreni, was close to the means of Zones 4, 5 and 6 for DAY2, DAYS and ASL, and started the growth two days earlier than the two provenances in Zone 4.

Table 3. — Results from analyses of variance based on model (2). The table shows p-values of F-tests.

Source	ASL	DAY1	DAY2	DAYS	RSE
Zone	0.015	<0.0001	0.001	<0.0001	0.87
Provenance (Zone)	<0.0001	<0.0001	<0.0001	<0.0001	0.067
Year	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Zone x year	0.27	0.05	0.80	0.97	0.12
Provenance (zone) x year	0.92	0.76	0.90	0.94	0.52
Replicate	<0.0001	0.0002	0.001	0.001	0.006
Year x replicate	0.72	0.001	0.88	0.74	0.69

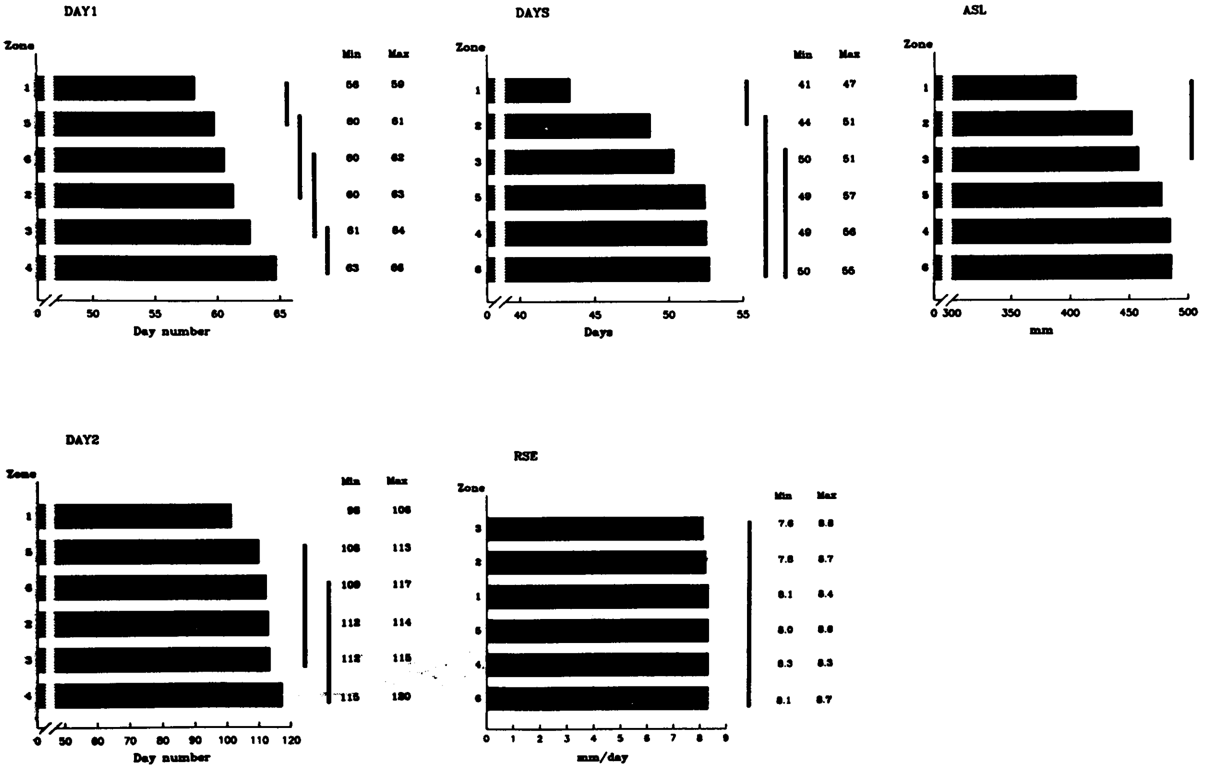

Figure 4. — Means of shoot elongation characteristics (DAY1, DAY2, DAYS and RSE) and annual shool length (ASL) for each of the 6 provenance zones, averaged over the 2 years. Means that are not significantly different ($p > 0.05$) are covered by a continuous vertical line. The minimum (MIN) and maximum (MAX) value within each zone are listed.

Rate of shoot elongation

The rate of shoot elongation, RSE, showed a variation pattern different from those of the variables characterizing the timing and duration of the elongation period. No significant differences were present for RSE, neither between nor within zones (*Table 3, Figure 4*).

Experimental error

The coefficients of variation from the ANOVA of model (2) show that the variables characterizing the timing of the elongation period has the smallest experimental error. For DAY1 and DAY2 this coefficient was 3.3% and 4.5%, respectively, while it was 8.9% for DAYS and 12.1% for both RSE and ASL.

Influence of altitude

Figure 5 shows plots of the variables DAY1, DAY2, DAYS, RSE and ASL against the altitude for the eight provenances along an altitudinal transect in the region in South Poland. There was a significant negative correlation with altitude for DAY2, DAYS and ASL, but not for DAY1 and RSE. The regression coefficients for the 2 years based on model (3), did not differ significantly, and a common regression coefficient was estimated. *Table 4* presents results from the regression analysis. The effect of the altitude on growth cessation, the length of the elongation period and annual shoot length was pronounced. The high altitude seed sources had, in most cases, a shorter growth period, an earlier growth cessation and less growth than the low altitude provenances within the region. No clear relationship existed between RSE and altitude.

Variation in lignification

The provenances means of unlignified annual rings for the 10 provenances studied were highly significant by the F-test ($p < 0.0001$), with a range of variation from 1.2 (Seljord, Norway) to 5.2% (Istebna, southern Poland). The multiple t-tests did not discern between the 3 provenances belonging to Zones 1 and 2, which, however, were found different from those from the more southern latitudes.

Correlation patterns

Phenotypic correlation coefficients among the different shoot growth variables, calculated both among provenance means and within provenances, based on residuals from the ANOVAS, are shown in *table 5*. There was a strong positive correlation between DAY2 and DAYS, but no strong correlation between DAY1 and DAY2. Both DAY2 and DAYS showed strong positive correlations to

Table 4. — Results from the regression analyses based on model (3). Shown are estimated regression coefficients b, their p-values and the squared correlation coefficients of the regression lines.

Variable	b	p-value	R^2
DAY1	- 0.0002	0.744	0.05
DAY2	- 0.0158	<0.0001	0.73
DAYS	- 0.0156	<0.0001	0.71
RSE	0.0005	0.13	0.03
ASL	- 0.101	0.0002	0.60

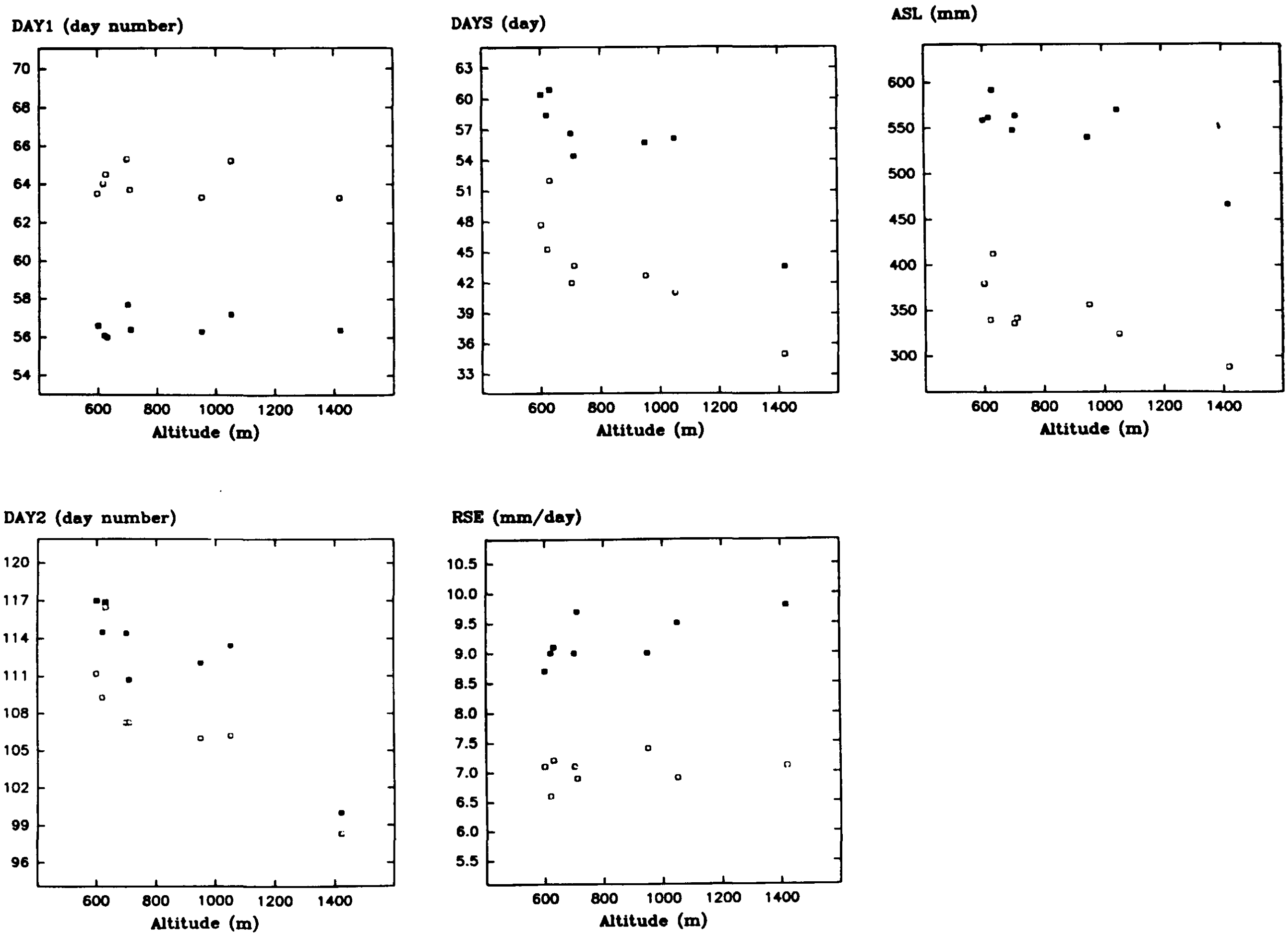

Figure 5. — Plot of shoot elongation characteristics (DAY1, DAY2, DAYS and RSE) and annual shoot length (ASL) against the altitude of the provenance for the 8 provenances from southern Poland. The 1979 values are denoted by open and the 1980 values by filled squares.

total shoot length (ASL). RSE was not significantly correlated to the other growth curve characteristics. The plot of ASL against RSE (*Fig. 6*) revealed that the Norwegian (#33), the Finnish (#29) and the high altitude provenance from southern Poland (1420m) (#24) behaved differently from the other provenances with short shoot lengths and above mean rates of elongation. When these three provenances were deleted from the calculations, the correlation coefficient between RSE and ASL increased from 0.46 to 0.70.

The relative contribution of DAYS and RSE to the variation in ASL, evaluated by the coefficient of determination, was calculated both at the provenance level and within provenances, i. e. at the plot mean level, based on all 36 provenances. At the provenance level, the duration of the elongation period, DAYS, was most important. It accounted for 80% of the variation between provenances in ASL, while RSE determined 20%. Within provenances, however, RSE accounted for 51% of the plot mean differences, corrected for block effects, and DAYS for 49%. This shows that the provenance differences in height growth mainly were related to differences in the duration of growth. Whereas the rate of growth and its duration are equally important for the within provenance differentiation in height growth.

Separate calculations were made within Zones 2 and 5, which contained 8 and 5 provenances, respectively. Within Zone 2 there were high and significant correlations between DAYS and ASL ($r=0.94$) and RSE and ASL ($r=0.88$), and the relative contribution from the 2 variables to the total shoot growth was 50% from each variable. Within Zone 5 the relationships between the characters were completely different. Still there was a high correlation between DAYS and ASL ($r=0.87$), but no relationship was present between RSE and ASL ($r=0.02$). Of the variation in shoot growth DAYS accounted for 98%.

A high positive correlation was present between the provenance means for lignification and DAY2 ($r=0.82$, $p=0.004$) and lignification and DAYS ($r=0.79$, $p=0.007$).

The correlation coefficient between total tree height of provenances after 9 years (end of 1982) and DAY2 and DAYS were $r=0.79$ ($p<0.0001$) and $r=0.82$ ($p<0.0001$), respectively. No significant relationships were present between the total height and DAY1 or RSE.

Correlations coefficients between the percentage of seedlings with visible terminal buds in the experiment in West-Norway and DAY2 were $r=-0.85$ ($p<0.0001$) based on the 16 common provenances (Magnesen, pers. com.). Between the height growth after 13 years in the field in West-Norway and DAY2 and DAYS the correlation coefficients were $r=0.69$ ($p=0.003$) and $r=0.66$ ($p=0.005$), respectively. No relationships were present between RSE and the traits measured in the other experiment.

Table 5. — Within- and among-provenance phenotypic correlations, and relative contributions of the duration of the shoot elongation period (DAYS) and rate of shoot elongation (RSE) to annual shoot length (ASL).

Variables	Within provenances	Among provenances
DAY1, DAY2	0.23	0.58
DAY1, DAYS	- 0.14	0.22
DAY1, RSE	- 0.12	- 0.23
DAY2, DAYS	0.93	0.92
DAY2, RSE	- 0.13	- 0.01
DAYS, RSE	- 0.09	0.10
DAY1, ASL	- 0.19	0.13
DAY2, ASL	0.59	0.82
DAYS, ASL	0.68	0.92
RSE, ASL	0.64	0.46
Relative contributions:		
DAYS	0.51	0.80
RSE	0.49	0.20

Discussion

Methodology

The shoot elongation of conifers has formerly been successfully described by logistic curves (Rehfeldt, 1986), Richards' function (Ford et al., 1987; Bridgwater, 1990), and by the Weibull function, which has been used in this study (Beckwith and Kemp, 1984; Perala, 1985; Magnussen and Yeatman, 1989). The Weibull is a flexible function that is well suited to model this type of biological data.

As the mean elongation pattern of provenances was the objective of this study, the curves were fitted to measurements made on plots of four trees and not to the shoot elongation data of each individual tree. This offers advantages: the number of curves to be estimated is reduced by 75% and a test of goodness of fit of each estimated function is available. If individual trees were to be selected for their growth pattern or individual tree heritabilities were to be estimated, then tree data might be preferred for the estimation.

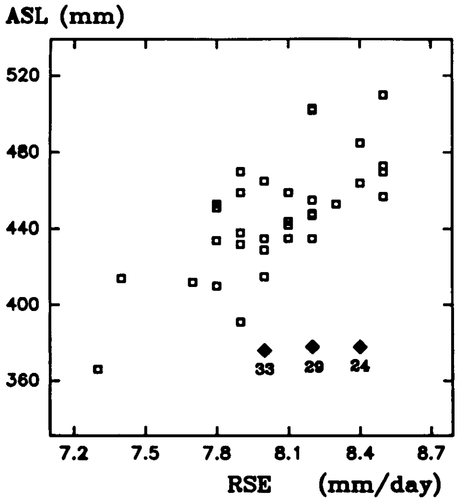

Figure 6. — Plot of annual shoot length (ASL) against relative shoot elongation (RSE). The 2 northernmost provenances (#33 and #29) and the high altitude provenance from southern Poland (#24) are denoted by filled diamonds.

The elongation characteristics DAY1, DAY2, DAYS and RSE depend on the definitions of growth initiation and cessation. Here the initiation of growth is defined as the day when first 20mm of growth is completed. As the elongation is measured from the basis of the shoot, this corresponds approximately to the stage when the elongating bud bursts, which corresponds to stage 4 in a classification scheme that is much used for flushing assessments of Norway spruce (Krutzsch, 1975). It is felt that this definition of growth initiation is more relevant than a fixed percentage of total shoot length, e. g. 5%. For the cessation of growth, the present definition is more arbitrary. Alternative calculations were made, defining the growth initiation and cessation at 5% and 95%, 10% and 90%, and 20% and 80% of total shoot length, respectively. However, identical conclusions regarding variation and correlation patterns emerged from these definitions.

Free growth and lammas growth contribute to the total shoot lengths of young Norway spruce plants and also influence their growth rhythms (e. g. von Wühlisch and Muhs, 1987; Ununger et al., 1988). In this experiment free growth was present on very few trees and can be ignored. Lammas growth occurred more frequently. However, as the portion of the shoot that resulted from lammas growth was not included in the elongation measurements, it has little effect on the estimated parameters.

Variation in shoot elongation and height growth

The traits that characterize the timing and duration of the shoot elongation period (DAY1, DAY2 and DAYS) expressed clear provenance differences with regional patterns of variation. Provenances from northern latitudes had both the earliest initiation and cessation of shoot growth and the shortest duration of the growth period. A similar pattern of variation was found among provenances from the altitudinal transect, with high altitude provenances having the earliest cessation and shortest duration of growth. The observed patterns correspond well with results from assessments of flushing and terminal bud-set in other Norway spruce provenance studies, both from field experiments and growth chambers (e. g. Langlet, 1960; Dietrichson, 1969; Dormling, 1973; Krutzsch, 1975, 1986). However, these studies did not have any estimates of the duration of the growth period.

The rate of shoot elongation (RSE) did not show any interpretable geographic pattern of variation. High RSE values were found both in low and high altitude provenances and in provenances from northern latitudes. The coefficient of variation was considerably higher for RSE than for the other growth curve characteristics. The difference in RSE between the 2 years 1979 and 1980 was also large. Environmental differences in soil and fertility and in climatic conditions between years therefore seem to have a larger influence on the rate of growth than on its cessation and duration. It was shown by von Wühlisch and Muhs (1987) that spacing may effect the rate of growth. They observed that shoots on densely spaced Norway spruce trees, grown in pots, elongated twice as fast and grew twice the lengths of shoots on widely spaced trees, in almost the same number of days.

Provenances with high ASL generally had a long shoot elongation period and a late cessation of growth, and the total shoot length was strongly associated with the duration of the elongation period. The variation among provenances in height growth therefore parallelled the provenance variation in duration and cessation of shoot growth and showed the same regional patterns.

The variation in ASL among plots within provenances was equally related to the duration (DAYS) and the rate of the shoot elongation (RSE). Main causes for this variability are within-provenance genetic variation and environmental differences among plots. The increased effect of RSE on within-provenance variability of shoot lengths corresponds with the larger environmental influence on this trait.

Interpreting provenance differences

The annual rhythm and total shoot growth of provenances grown in common garden experiments are determined both by their inherited adaptive properties and by effects of provenance transfers. The adaptation to the climatic conditions adjusts the growth season of the plants to the frost free period and secure the attainment of winter hardiness in due time. Photoperiod and temperature are the environmental factors that initiate and control the annual growth rhythm of northern conifers (Vaartaja, 1959; Holzer, 1978; Ekberg et al., 1979). When Central European spruce provenances are planted at a northern site, they experience a prolonged photoperiod which generally will delay their growth cessation (Magnesen, 1972). Such transfer effects may affect provenances differently, depending on the distance of transfer. It is also known that the temperature conditions in one specific year may influence both the growth intitiation and amount of shoot growth the succeeding year (Heide, 1974).

Norway spruce has a long history of extensive planting in Central Europe (Schmidt-Vogt, 1977), which makes it difficult to discern between autochthonous and non-autochthonous stands. Differences in performance between provenances from the same region may therefore not exclusively express adaptational differences. Pollen exchange between stands may in addition influence their genetic differentiation, in particular in the mountainous areas.

The observed regional differences in the timing, duration and total amount of annual shoot growth may therefore be due to several of these factors, which also may interact. Regional adaptations to climatic conditions, however, are likely to be most important, in particular as our results correspond with growth rhythm observations made under controlled conditions in climate chambers. Such studies have identified clinal variation in photoperiodic response among Norway spruce populations from different latitudes, longitudes and altitudes (e. g. Magnesen, 1972; Dormling, 1973; Ekberg et al., 1979). Climatic adaptation, however, does not preclude that other traits also are selected for, in particular in areas with a mild climate where low temperatures at the beginning and the end of the growth period are not critical. As competition for light is an important factor and being a tall tree may be a selective advantage, height growth is such a trait. A superior tree height may most easily be achieved by having a long growth season where early autumn frosts normally do not occur. However, at northern latitudes or at high altitudes a more intense growth in a shorter period may be more beneficial. Such differences may explain why the 3 provenances #24, #29 and #33 failed to fit in the general relationship between ASL and RSE.

Differences in within-zone variability were found between Zone 5 (Southern Poland) and Zone 2 (Latvia). In Zone 2 both DAYS and RSE were important for determining the provenance differences in ASL, while only DAYS were important in Zone 5. Zone 5 contains a large topographic variation with corresponding climatic differences. This may have caused adaptational differences among populations that are geographically close. Such differences may be the reason for the variability in height growth within this zone. In Zone 2 the topography is much less variable and the between-provenance variability in height growth within this zone may have other causes than differential climatic adaptations. The spruce in the two zones has different evolutionary histories, as provenances from southern Poland are thought to originate from a refugium in the Carpathian mountains during the last glaciation, whereas the Latvian spruce has its origin in a Russian refugium (Schmidt-Vogt, 1977). Differences in the amount of genetic variability at allozyme loci in spruce from the 2 regions were found by Lagercrantz and Ryman (1990), who interpreted these and corresponding differences in morphological traits as effects of migration and drift, rather than local adaptations.

Relationships among traits

Strong relationships were found at the provenance level among cessation of elongation, lignification and terminal budset, even if the measurements were made under different environmental conditions and different ages. These traits are components of an annual sequence of developmental events (Rehfeldt, 1986), which describes the annual rhythm of the tree. Such traits are therefore generally interrelated, in particular if they are triggered by the same environmental factor, e. g. temperature or photoperiod. The coherence is, however, never complete, in particular when provenances experience different geographic transfers, which may change the normal relationships between adaptive environmental factors. Also the relative rate of development for two events, such as cessation of shoot elongation and the subsequent attainment of frost hardiness, may vary among provenances. These differences may have important implications if the first trait, e. g. cessation of elongation, is being used to assess the risk of frost damage by early autumn frost. A better knowledge of the relationships between the traits and how they depend on changed environmental conditions is therefore required.

Implications for choice of provenances and breeding

It is possible to identify zones which in general have a late initiation of shoot growth. This has been utilized in Sweden, where the use of late flushing north-east European spruce provenances is recommended on sites where late spring frost is a problem (Werner et al., 1991). Apart from this, the large variation among provenances within zones for both growth cessation and height growth makes the zones less suitable for general provenance recommendations. Instead, seed from smaller areas or single stands that have proven their performance should be used. The best-growing provenances will in general have a long elongation period with a late cessation. Therefore a compromise will have to be made between the selection for superior growth and a well-timed elongation period. The importance of the date for growth cessation should be determined by a closer examination of the relationships between DAY2 and frost hardiness, e. g. in artificial freezing tests. In addition, if high wood quality is a concern, possible negative effects of a late cessation of shoot growth on wood density, should be investigated. For the climatic conditions at low altitudes in south-eastern Norway selection among provenances in Zone 2 seems to be an optimal choice.

Large variation is present within Norway spruce populations for the shoot elongation characteristics (Ekberg et al., 1985; Skrøppa, 1982). Breeding values of these traits should therefore be considered when individuals are selected to be included in breeding populations. Indications are given that genetic differences in RSE are more important among families than among provenances for determining height growth differences (Skrøppa, unpublished), as also has been found for other species (Magnussen and Yeatman, 1989). The rate of shoot elongation may therefore be an important trait in Norway spruce breeding programs.

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