Swedish University of Agricultural Sciences
Faculty of Forestry
Uppsala, Sweden

Between- and within-population variation in growth rhythm and plant height in four *Picea abies* populations

INGER EKBERG, GÖSTA ERIKSSON & YUEXIA WENG

Department of Forest Genetics

Studia Forestalia Suecica
No. 167 · 1985

ISSN 0039-3150
ISBN 91-576-2233-7

Abstract

Ekberg, I., Eriksson, G. & Weng, Yuexia. 1984. *Between- and within-population variation in growth rhythm and plant height in four* Picea abies *populations.* Studia Forestalia Suecica 167, 14 pp. ISSN 0039-3150, ISBN 91-576-2233-7.

Cones were collected from 21 trees in each of four Swedish, geographically widely distributed populations of *Picea abies* (L.) Karst. during the rich cone crop year 1977. Plant height as well as growth rhythm recorded as bud-flushing, bud-set, attainment of 50% or 80% growth of the leader, and duration of the growth period were studied in a nursery at Uppsala during the years 1979–1982. The analysis of variance revealed strongly significant between- and within-population differences with respect to most of the growth rhythm characters studied during 1981 and 1982 when the plants were well established at the test site. The within-population variation was lower in the northern population than in the others. The difference within populations for leader length and plant height was in most cases non-significant. Family repeatabilities based on means for growth rhythm characters varied between 0.5 and 0.9 in 1982 when the estimates were highest. The family repeatabilities for plant height and leader length never exceed 0.3 but the experimental errors were large. There were strong genetic correlations between the growth rhythm characters. The genetic correlations for the same character between years 1981 and 1982 were strong.

Key words: Picea abies, growth rhythm, plant height, between- and within-population variation, genetic correlations.
ODC 232.12:174.7 *Picea abies.*

Inger Ekberg and Gösta Eriksson, Swedish University of Agricultural Sciences, Department of Forest Genetics, P.O. Box 7027, S-750 07 Uppsala, Sweden.

Yuexia Weng, Subtropical Forestry Res. Inst., The Chinese Academy of Forestry, Fuyang, Zhejiang, The People's Republic of China.

Content

MS. accepted 8 January 1985

Tofters tryckeri ab, Östervåla 1985

Introduction

The information on genetic variation in native *Picea abies* populations in Sweden is limited. The magnitude of variation within and between populations is of importance in choosing the breeding programme. Both the variation in adaptive traits such as growth rhythm, and the genetic correlation between characters of economic value, need to be estimated. Only one report on genetic correlations of characters in *Picea abies* is known to us (Dietrichson 1971*a*).

There are reports on the genetic variation within introduced populations of *Picea abies* (Lindgren & Eriksson, 1976). They studied the bud-flushing of Polish and Slovakian populations. The variation within populations was larger than the variation between the population means.

From the study of the inheritance of bud-flushing and bud-set in seedlings of *Picea abies* by Eriksson et al. (1978) it is evident that there is a large within-provenance variation. Analogous results were also reported by Ekberg et al. (1982) in their study of tree height and tree volume of *Picea abies* inter- and intra-provenance families.

The quoted papers deal all with characters of economic interest. The knowledge of variation with respect to characters of non-economic interest is scanty except for isozymes (cf. Lundkvist, 1979).

For many of the growth rhythm characters studied in temperate conifers, the variation between families was larger or of the same magnitude as the variation among populations. This was the case for *Abies lasiocarpa* (Dietrichson, 1971*b*), *Picea abies* (Dietrichson, 1969*b*), *Picea glauca* (Pollard & Ying, 1979*a*), *Picea mariana* (Dietrichson, 1969*a*), *Pseudotsuga menziesii* (Rehfeldt, 1974*b* , 1983; Campbell, 1979) and *Pinus sylvestris* (Wright, 1963). As regards *Pinus contorta* significant differences between families were observed for formation of anthocyanin but not for degree of lignification or dry matter content (Dietrichson, 1970). The between-population variation was significant for all three characters.

With respect to height, the within-family variation was larger or of the same size as the among-population variation in most of the studies cited above including Rehfeldt (1974*a*, *Pseudotsuga menziesii*, two-year height) and Pollard & Ying (1979*b*, *Picea glauca*, seedling height at age 12, 20, and 37 weeks). Exceptions are the four-year height and leader length (Rehfeldt, 1983) and three-year height (Campbell, 1979) in *Pseudotsuga menziesii* and height at age seven and leader length for two years in one of the *Picea abies* populations studied by Dietrichson (1969*b*). The family heritability varied between 0.30 and 0.87 for growth rhythm characters, seven-year height and leader length in *Picea abies* (Dietrichson, 1969*b*), between 0.18 and 0.42 for one-year and four-year height in *Picea mariana* (Morgenstern, 1974), between 0.51 and 0.82 for growth rhythm characters and height at age two in *Pinus sylvestris* (Wright, 1963), between 0.61 and 0.81 for growth rhythm characters and four-year height and leader length in *Pseudotsuga menziesii* (Rehfeldt, 1983), in *Picea glauca* the family heritability for tree height at age ten was reported to be 0.39 (Dhir, 1976). The figures given above are not directly comparable since different ways of calculation were used.

The purpose of the present study is to throw more light on the variation between *Picea abies* populations for traits of economic interest that may be of value for tree breeding and gene conservation. To obtain the information we collected cones on 21 trees in four geographically widely separated (lat 56–64°) populations of *Picea abies* in the rich cone crop year 1977.

Material and methods

Experimental design

In 1977 open-pollinated seeds were collected from 21 parent trees in each of four Norway spruce populations, located in southern, northern, eastern, and western Sweden, respectively. Location and elevation of each stand is shown in Table 1.

The seedlings were grown in a greenhouse during their first growth period. After bud maturation and breakage of the bud dormancy, the plants were transplanted to a nursery in June 1978.

A randomized complete block design was used with four replications. In each replication, the half-

Table 1. *Location of the four Norway spruce populations included in the analysis*

Population	Province	Latitude	Longitude	Altitude
7	Ångermanland	64° 13′	16° 11′	350 m
6	Uppland	59° 59′	17° 26′	40 m
4	Värmland	59° 42′	12° 59′	134 m
5	Skåne	56° 25′	14° 27′	135 m

sib families were randomized regardless of the population they belonged to. Eight-tree plots were used. The spacing was 0.5 m × 0.5 m. In some plots less than eight plants were recorded owing to plant death or abnormal leader growth. Only apical shoots or lateral shoots that grew like a leader were included in the analysis.

No recordings were made during the first growing season in the nursery. During the subsequent four growing seasons, 1979–1982, the bud-flushing and bud-set were recorded, usually once a week. The growth of the terminal shoots were in most cases measured every second week during the period of rapid growth except for 1981 when only the final length of the terminal shoot was measured. The final plant height was recorded at the end of each growing season in 1979–1982.

The different developmental stages of the terminal buds were classified according to a scheme originally published by Krutzsch (1973). It has been slightly modified in the present study:

Score	Stage of development
000	Dormant buds
100	Buds slightly swollen, needles below buds bent backwards and outwards
200	Buds swollen, green to grey-green in colour, bud scales still closed
300	Burst of bud scales, tips of needles emerging
400	Elongation of needles to double or three times the bud length
500	Elongation of needles to four times the bud length or longer
510	Formation of lateral buds, white-greenish, on the leader
710	Appearance of terminal buds.

The variables regenerated from the recordings in the nursery and used in the statistical analyses are listed in Table 2.

The growth rhythm variables were regenerated from the recordings made in the nursery. These variables have been expressed both on a D (day) scale and on a T (temperature sum) scale. The D scale implies that the mean number of days for reaching the various bud stages and for reaching 50% or 80% of the final leader length have been calculated. The technique used for these calculations was presented by Eriksson et al. (1978, Table 3). The mean number of days between two consecutive recordings was multiplied by the proportion of plants that had reached a specific bud stage at the later recording but not at the earlier one. The products thus obtained were then summed. On the D scale, day number one equals May 1st. The first day of recording, however, varied in different years.

Table 2. *The variables regenerated from the recordings in the nursery and used in the statistical analyses*

Variable	Year			
	1979	1980	1981	1982
D300	x	x	x	x
T300	x	x	x	x
D400	x	x	x	x
T400	x	x	x	x
D500	x	x	x	x
T500	x	x	x	x
D510			x	x
T510			x	x
D710		x	x	x
T710		x	x	x
D 50%	x		x	x
T 50%	x		x	x
D 80%	x		x	x
T 80%	x		x	x
D 80%–D400	x		x	x
T 80%–T400	x		x	x
Leader length	x	x	x	x
Plant height	x	x	x	x

The mean temperature sums for reaching the individual bud stages, as well as 50% and 80% of the final leader length, were calculated in a corresponding way. The initial day for starting the calculation of the temperature sums was the first of four consecutive days when the daily mean temperature exceeded +6°C (Perttu and Huszár, 1976). From that day on, all temperatures exceeding +6°C were summed. In the years 1980–1982 this day occurred some time during the three last weeks in April, but in 1979 it was delayed until May 11th.

Statistical analyses

Analysis of variance and estimation of variance components

The linear model used was as follows:

$$y_{ijkl} = \mu + \alpha_i + \beta_{j(i)} + r_k + (\alpha r)_{ik} + p_{ijk} + w_{ijkl}$$

where

y_{ijkl}	= an observation of one plant
μ	= grand mean
α_i fixed	= population effect; $i = 1, 2, 3, 4$
$\beta_{j(i)} \sim N(0,\sigma^2_\beta)$	= family effect within population; $j = 1, 2 \ldots 21$
$r_k \sim N(0,\sigma^2_r)$	= replication effect; $k = 1, 2, 3, 4$
$(\alpha r)_{ik} \sim N(0,\sigma^2_{\alpha r})$	= interaction between population and replication
$p_{ijk} \sim N(0,\sigma^2_p)$	= plot effect
$w_{ijkl} \sim N(0,\sigma^2_w)$	= random error within plot = the remainder of the genetic effect between half-sib plants on the same plot and the environmental effect; $l = 1, \ldots, n_{ijk}$; $1 \leq n_{ijk} \leq 8$.

ANOVA

Source	*df*	EMS
Population	$a-1$	$\sigma^2_e + b\sigma^2_{\alpha r} + c\sigma^2_\beta + bc\sigma^2_\alpha$
Family within population	$a(b-1)$	$\sigma^2_e + c\sigma^2_\beta$
Replication	$c-1$	$\sigma^2_e + b\sigma^2_{\alpha r} + ab\sigma^2_r$
Population × replication	$(a-1)(c-1)$	$\sigma^2_e + b\sigma^2_{\alpha r}$
Plot	$a(b-1)(c-1)$	$\sigma^2_e = \sigma^2_w + C\sigma^2_p$
Error within plot	$\Sigma_{ijk}(n_{ijk}-1)$	σ^2_w
Total	$\Sigma_{ijk} n_{ijk}-1$	

σ^2_α denotes $\dfrac{\Sigma_1^a(\alpha_i-\bar{\alpha})^2}{a-1}$

$$C = \left(\frac{1}{abc} \Sigma_{ijk} n_{ijk}^{-1} \right)^{-1}$$

Analysis of variance was performed according to the SAS, PROC. GLM and PROC. VARCOMP using the fitting constant method to estimate the variance components.

EMS was only roughly equal to the above given formulae as the n_{ijk} varied slightly. C (the harmonic mean) was within the interval 5.8–6.6 for 1980–1982 and 3.4–4.0 for 1979.

Family repeatability was estimated on an individual tree basis by

$$h^2_{fam} = \frac{\sigma^2_\beta}{\frac{\sigma^2_w}{rC} + \frac{\sigma^2_p}{r} + \sigma^2_\beta}$$

Correlation analysis

Both genetic and phenotypic correlations between different characters within each year and between the same character two different years have been performed. Each population was treated individually. The calculations are based on plot means.

GENETIC CORRELATIONS

For correlations between two characters, the model used was as follows

$$\begin{bmatrix} \bar{x}_{jk.} \\ \bar{y}_{jk.} \end{bmatrix} = \begin{bmatrix} \mu_x \\ \mu_y \end{bmatrix} + \begin{bmatrix} \beta_j(x) \\ \beta_j(y) \end{bmatrix} + \begin{bmatrix} r_k(x) \\ r_k(y) \end{bmatrix} + \begin{bmatrix} e_{jk}(x) \\ e_{jk}(y) \end{bmatrix}$$

where

$$\begin{bmatrix} \beta_j(x) \\ \beta_j(y) \end{bmatrix} \sim N\left(0, \begin{bmatrix} \sigma^2_\beta(x) & \sigma_\beta(x, y) \\ \sigma_\beta(x, y) & \sigma^2_\beta(y) \end{bmatrix} \right)$$

$$\begin{bmatrix} r_k(x) \\ r_k(y) \end{bmatrix} \sim N\left(0, \begin{bmatrix} \sigma^2_r(x) & \sigma_r(x, y) \\ \sigma_r(x, y) & \sigma^2_r(y) \end{bmatrix} \right)$$

$$\begin{bmatrix} e_{jk}(x) \\ e_{jk}(y) \end{bmatrix} \sim N\left(0, \begin{bmatrix} \sigma^2_e(x) & \sigma_e(x, y) \\ \sigma_e(x, y) & \sigma^2_e(y) \end{bmatrix} \right)$$

The genetic correlation is estimated by

$$\hat{\varrho}_\beta(x, y) = \frac{\hat{\sigma}_\beta(x, y)}{\hat{\sigma}_\beta(x) \cdot \hat{\sigma}_\beta(y)}$$

where

$$\hat{\sigma}_\beta(x, y) = \frac{\hat{\sigma}^2_\beta(x+y) - \hat{\sigma}^2_\beta(x) - \hat{\sigma}^2_\beta(y)}{2}$$

(see Kempthorne, 1973).

The variance component for the sum $\hat{\sigma}^2_\beta(x+y)$ was estimated by using SAS PROC. VARCOMP.

$\hat{\sigma}^2_\beta(x)$ and $\hat{\sigma}^2_\beta(y)$ were taken from the univariate analysis.

In some cases the absolute value of the correlation coefficient exceeded 1. This could be attributed to the method used and occurred when one of the variance components—$\hat{\sigma}^2_\beta(x)$ or $\hat{\sigma}^2_\beta(y)$—was very small compared to the other.

PHENOTYPIC CORRELATIONS

For comparison interclass correlations were estimated by

$$\hat{\varrho}_{ph}(x, y) = \frac{\Sigma_{jk}(\bar{x}_{jk.} - \bar{x}...)(\bar{y}_{jk.} - \bar{y}...)}{\sqrt{\Sigma_{jk}(\bar{x}_{jk.} - \bar{x}...)^2 \Sigma_{jk}(\bar{y}_{jk.} - \bar{y}...)^2}}$$

These correlations may be regarded as some type of phenotypic correlations. They were tested in the usual way.

Results

From Figures 1–2 a visual impression of the variation within and between populations with respect to different types of characters may be obtained.

Analysis of variance

The results as regards the significance of different growth rhythm characters are illustrated for 1982 in Table 3. In this table the significance between families within stands is shown separately. Moreover, the family repeatabilities based on populations 4–6 and 4–7, respectively, are given.

The variance components (population, family, individual, environmental) are visualized in Figure 3 for the analysis based on populations 4–6.

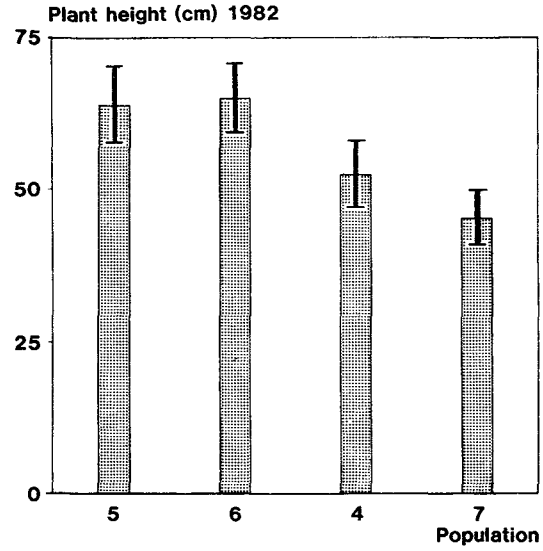


Fig. 2. Plant height in 1982. Mean value ± standard deviation.

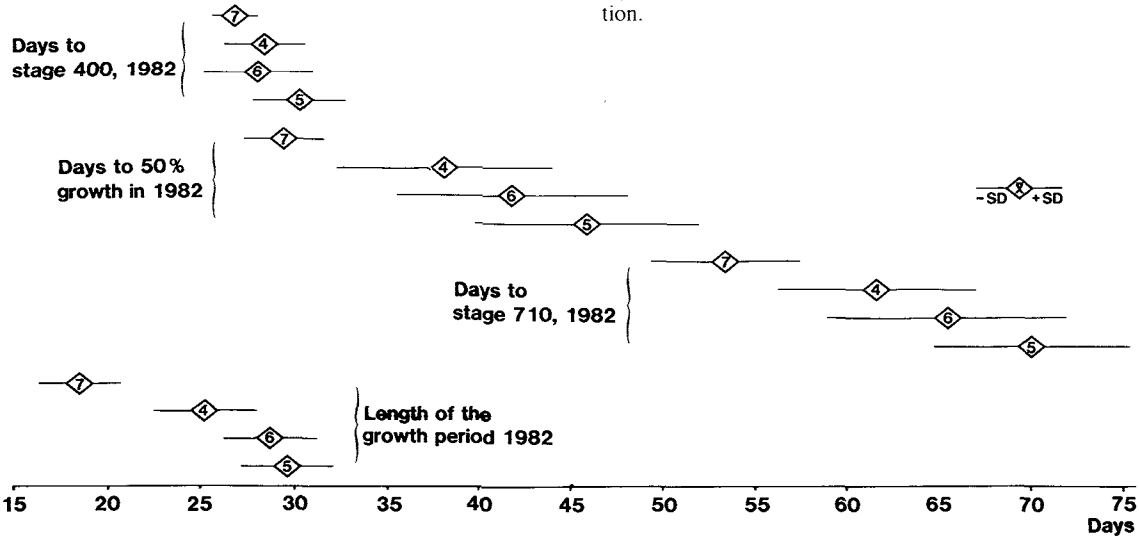


Fig. 1. Time for attainment of bud-flushing stage D400, D50% growth, and bud-set stage D710, mean numbers of days from May 1st in 1982 ± standard deviation and the mean duration of the growth period in 1982 ± standard deviation. The populations are arranged from north (above) to south (below).

Correlations

We have selected for presentation the phenotypic and genetic correlations for the different characters based on the assessments during 1982 for population 4 (Table 4). Correlations for the years 1979–1981 will be commented on in the discussion.

The correlations for attainment of stages D 400 and D 710 between years are illustrated in Figure 5. There was a good agreement between the correlations based on mean number of days and degree days, so we chose to illustrate correlations based on mean number of days.

Discussion

One striking observation is that the results were more or less the same whether they were estimated on a day scale or a temperature sum scale. Our explanation is that temperature sum and number of days describe the pattern of growth rhythm equally well. Therefore, we will only present data based on number of days for the various growth rhythm variables.

ANOVA

The variance component for error is large. It could have been reduced by increasing the number of plants in the experiment or by reducing the number of plants within plots and increasing the number of replicates and possibly by shorter intervals between the assessments. Neither of these alternatives were feasible—a larger experiment would have caused the assessment to be extended over more than two days. Already with assessments lasting two days we may introduce an error during warm weather conditions when a rapid development takes place.

There is a clear tendency for the purely genetic components (=between-population and family-variance components) to increase with age. This could be attributed to problems with plant establishment. Some plants suffered from frost causing a big experimental error during the first years.

There is a slight tendency for an increase in the purely genetic variance components towards the end of the growing season. The later stages can be more accurately determined during the examination than the bud-flushing stages. Large genetic components for attainment of 50% and 80% of the total growth were noted for years 1981 and 1982 in the analysis based on data from all four populations.

The interaction replications × populations was in most cases non-significant.

Variation between and within populations

The results presented from the degree of significance (Table 3) and the variance components (Fig. 3) give the information on the relative importance of the two sources of variation.

There was a significant difference between the four populations for all characters studied. In most cases a strongly significant difference was obtained. These differences could in many cases be attributed to the difference between the northerly population (7) and the other populations (see lines 1 and 2 in Table 3). There seems to be a tendency towards a greater variation between the three southerly populations with increasing age. This might be attributed to problems with even establishment in the nursery during the first years of this experiment.

Our results agree with earlier published data on the growth rhythm of Scandinavian conifers, in which a change from linear to exponential differentiation around latitude 60° was obtained. Above latitude 60° the critical night length for bud-set in *Picea abies* decreases in an exponential way with latitude (Dormling, 1979). In *Pinus sylvestris* a similar pattern is obtained for plant survival above latitude 60° (Eriksson et al., 1980; Eriksson, 1982).

Below we shall first comment on the relative importance of the between-population variation and within-population variation when all four populations are included in the analysis. After that the same question will be treated for the three southerly populations.

FOUR POPULATIONS

For the stages of bud-flushing (300–500) the family-variance component was larger than the population component for all years except 1981. In that year, the difference between the mean values for the bud-flushing stages of the two extreme populations—Nos. 5 and 7—was largest (Fig. 4). This in turn could be attributed to the weather conditions with the highest temperature sums during April–May in 1981. This temperature sum was almost twice as large in 1981 as in 1980. That we attribute this to the weather conditions and not to an effect of age is based on our

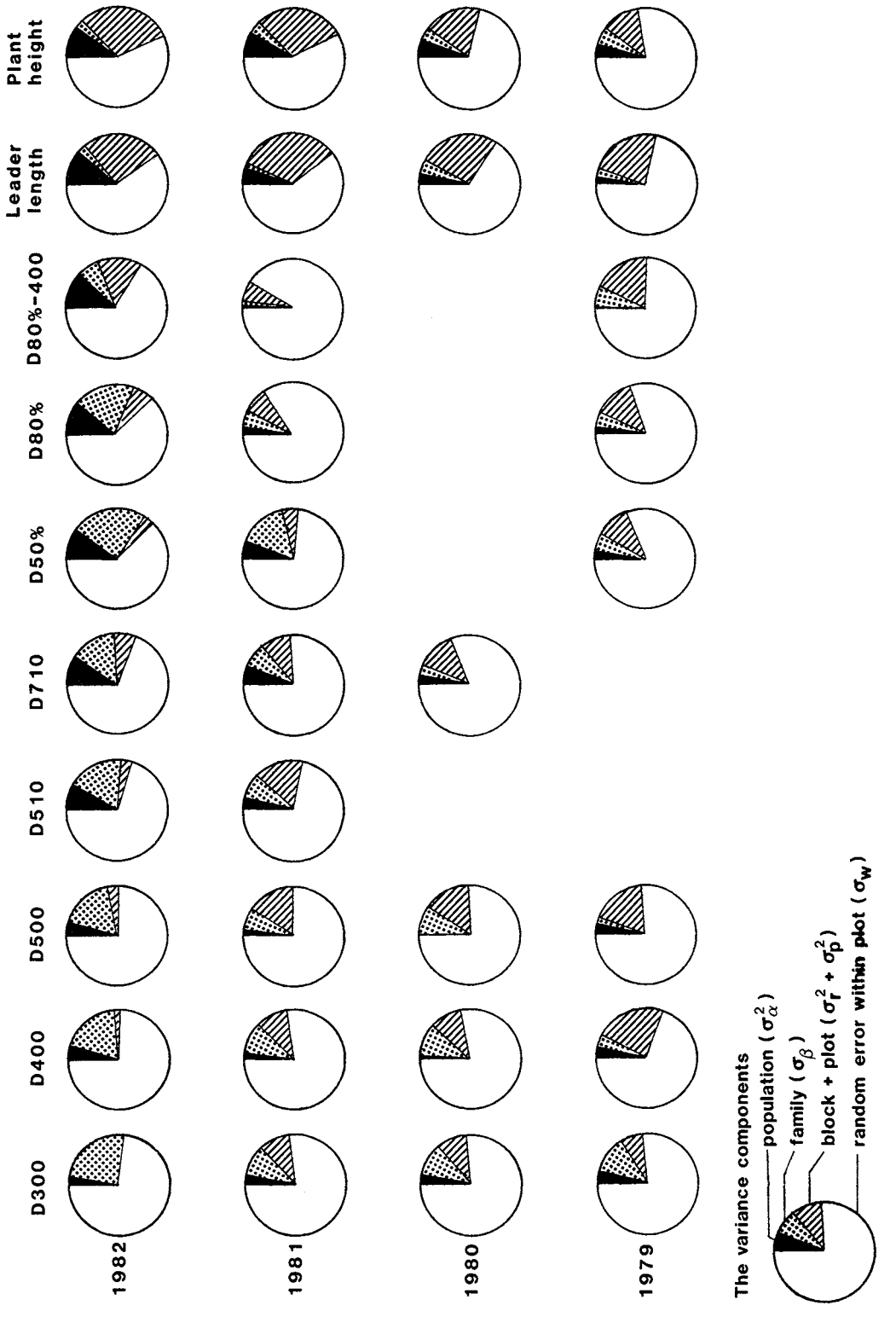


Fig. 3. Variance components for different characters of growth rhythm and growth based on a day scale for populations 4–6. The characters are arranged in chronologic order from left to right.

Table 3. *The results from the analyses of variance – four and three populations respectively – for all characters studied in 1982*
ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

	DF	D300	T300	D400	T400	D500	T500	D510	T510	D710	T710	D50%	T50%	D80%	T80%	D80%–400	T80%–400	Leader length	Plant height
Populations (4–7)	3	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Populations (4–6)	2	ns	*	*	*	*	*	***	***	***	***	***	***	***	***	***	***	***	***
Families in populations	80	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	ns	*
Families in population 4	20	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	*	*	ns
Families in population 5	20	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	*	ns	ns
Families in population 6	20	***	***	***	***	***	***	***	***	***	***	***	***	***	***	**	*	ns	ns
Families in population 7	20	**	**	ns	ns	**	***	ns	ns	**	**	**	**	***	**	*	ns	ns	ns
Replications	3	ns	ns	ns	ns	ns	*	*	**	*	*	ns	ns	ns	ns	***	**	**	***
Replications x populations	9	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
$h^2_{fam.}$ (pop. 4–7)		0.88	0.88	0.83	0.84	0.83	0.84	0.84	0.84	0.77	0.77	0.88	0.87	0.84	0.85	0.59	0.47	0.24	0.26
$h^2_{fam.}$ (pop. 4–6)		0.91	0.90	0.87	0.87	0.85	0.87	0.87	0.87	0.81	0.80	0.89	0.89	0.86	0.86	0.59	0.48	0.25	0.24

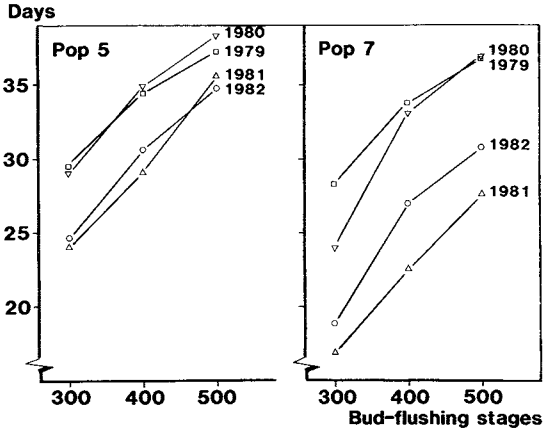


Fig. 4. Number of days from May 1st for attainment of bud-flushing stages D300, D400 and D500.

knowledge that under controlled conditions the date for flushing occurs later with increasing age (Ununger & Ekberg, in preparation).

At the end of the growing season (stages 510 and 710) the population component was larger than the family component. The same was true for the attainment of 50% and 80% of the growth and particularly for the duration of the growth period, leader length and total plant height.

These results are of course also reflected in the results of the ANOVA, in which there were hardly ever any significant differences on the family level within populations for leader length or plant height.

One striking observation is that there is less variation among the families of the northerly population (7) than among the families of the other populations. However, there is a tendency for a larger variation within population 7 with increasing age. One reason for the low variation within population 7 might be that bud-flushing and shoot elongation is a rapid process in this population which was transferred southwards four degrees of latitude. Our weekly assessments might not reveal all the variation existing within this population.

THREE POPULATIONS

Except for the results from 1979 the family variance components for the bud-flushing stages (300–500) were several times higher than the population components.

For bud-set and growth cessation (510 and 710) the family variance components were larger than the population variance component, which is in contrast to the results based on the four populations. This is a consequence of the early bud-set of population 7. The same was true for attainment of 50% and 80% growth.

For leader length and plant height the family component was smaller than the population component during 1981 and 1982 whereas the opposite was the case in three instances out of four in 1979 and 1980.

Comparison with other studies on growth rhythm

Our data agree with earlier reports on within-population variation in *Picea abies*. Thus Skrøppa (1982), in his preliminary report on growth rhythm variation within and between populations of *Picea abies* from a limited geographic area, showed that the variation within population exceeded the difference of population mean values. Eriksson (1982) reported a great within-population variation in bud-flushing of Polish and Czechoslovakian populations of *Picea abies* studied in nurseries. Our studies on growth rhythm in climate chambers of full-sib families also suggest a great within-population variation of *Picea abies* populations (Eriksson et al., 1978). This within-population difference remains at higher ages as a variation in vigour (cf. Engsjö et al., 1978; Ekberg et al., 1982).

It is evident that the traits of high adaptive value show a larger within-population variability than characters such as growth capacity. For traits of high climatic adaptive value in long-lived species such as our conifers a large within-population variation is expected as an adaptation to the environmental variation over time. This agrees with the model for fitness developed by Levins (1963). Moreover, this has been confirmed by all gene-ecological studies on conifers in Sweden carried out so far (cf. Eriksson, 1982). Recently Ståhl (1984) confirmed these results for the variation of growth rhythm in *Pinus sylvestris*.

Family repeatability

Generally the repeatability estimates were low for year 1979 and high for 1982 except for leader length and total plant height. With increasing age it is probable that the plants become more and more adapted to the microsites where they were planted. Therefore, the impact of the environmental conditions on the characters becomes less important, so that the phenotypic variance is reduced and the repeatability correspondingly increased.

The increase of the repeatability with time means that selection ought to be postponed until a certain stability is reached in the experiment. Therefore, we shall mainly refer to the repeatability estimates from 1982 when comparing the repeatabilities of different characters.

As seen from Table 3, all repeatabilities for growth

rhythm characters are above 0.7 except for the duration of the growth period. The repeatabilities for leader length and total plant height on the other hand were low, not exceeding 0.26. In contrast to the other characters, there is a weak tendency to a decrease of the repeatability with age. Franklin (1979) reported on a drop of the heritability at the end of the phase of establishment. This might be attributed to the individual and non-genetic adjustments of the plants to the microsites where they are growing, as well as to a genetically caused change due to different ratios of free and predetermined growth of different genotypes. It cannot be determined if the slight decrease in repeatability is of the same type as discussed for some American conifers by Franklin (1979). However, they might well be the same.

The only report known to us on family repeatabilities in *Picea abies* for the same type of characters as studied by us is that of Dietrichson (1969*b*). He reported on repeatabilities for growth rhythm and growth capacity of seven-year-old plants of families from stands in two different regions in Norway. The family repeatabilities reported by him were of the same magnitude as those obtained by us. As in our material the highest repeatabilities were obtained for flushing. It has to be mentioned that Dietrichson used another formula for estimating the family repeatabilities.

Correlations

The characters may be grouped into two bigger or five smaller groups:

Growth rhythm	
bud-flushing	D300, T300, D400, T400, D500, T500
bud-set	D510, T510, D710, T710
percentage growth	D50%, T50%, D80%, T80%
length of the growth period	D80%–D400, T80%–T400
Plant growth	
growth capacity	leader length, plant height

Between-character correlations of the same year

The genetic correlations, which are more complicated to estimate than the phenotypic correlations from a statistical point of view, are presented in Table 4 without notifying any statistical significance. The reason for this is that there is no simple way to test the genetic correlations in the presence of environmental correlations. However, the genetic correlations showed unambiguous results.

The genetic correlations, in which one of the characters did not show any significant variance component, are uncertain. They are shown within brackets in Table 4. In 1979 many of the genetic correlations were uncertain. With increasing age the number of non-significant characters declined gradually.

Two conspicuous features were noted when examining the genetic correlations. The first is the difference between the northerly population (7) on the one hand and populations 4–6 on the other hand. The second is the high level of genetic correlations within type of character analysed.

Table 4. *Phenotypic correlations (above diagonal line) and genetic correlations (below diagonal line) between different characters of growth rhythm and growth capacity for population 4 in 1982*

	D300	D400	D500	D510	D710	D50%	D80%	D80%–400	Leader length	Plant height
D300		.81***	.77***	.65***	.45***	.76***	.70***	.36***	.00^{ns}	.05^{ns}
D400	.98		.84***	.73***	.56***	.72***	.60***	.11***	−.18^{ns}	−.09^{ns}
D500	.89	1.01		.82***	.55***	.71***	.60***	.21***	−.24*	−.16^{ns}
D510	.86	.92	.97		.54***	.71***	.65***	.34***	−.11^{ns}	−.00^{ns}
D710	.77	.73	.86	.87		.63***	.54***	.31***	.09^{ns}	−.01^{ns}
D50%	.90	.96	.94	.92	.86		.96***	.74***	.40***	.38***
D80%	.91	.94	.90	.91	.82	1.00		.86***	.53***	.52***
D80%–400	.76	.80	.71	.82	.83	.93	.96		.78***	.70***
Leader length	.06	.02	−.12	−.07	.35	.24	.29	.50		.91***
Plant height	(.20)	(.20)	(.02)	(.06)	(.40)	(.38)	(.46)	(.66)	(.99)	

*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = not significant.
The figures in parantheses indicate that no significant variation was found at the family level for at least one of the characters.

Since the genetic correlations are dependent on gene frequences and the environmental conditions under which the study was carried out, it may be suspected that population 7 shows another pattern of genetic correlations than the other populations. Thus, the differences within population 7 showed a lower degree of significance than was the case for populations 4–6.

It is of course logical to expect a high genetic correlation between characters belonging to the same group of characters. It is rather hard to imagine the reverse situation. The genes responsible for onset of bud development, for example, all act in the same way with respect to characters D300, D400 and D500.

In populations 4–6 the genetic correlations between all the characters that might be described as growth rhythm characters were found to be high. This means e.g. that late bud-flushing is correlated with late bud-set. This contrasts with the results reported for *Pseudotsuga menziesii* seedlings studied by Rehfeldt (1983). He found no genetic correlation between bud-flushing and bud-set. *A priori* one might expect any of the two types of genetic correlations observed.

On the population level one might expect to find a negative correlation between bud-flushing and bud-set, thus causing an adaptation on the population level to different lengths of the growth period. The adaptation on the population level must be caused by disruptive selection whereas a stabilising selection may act within a population. This may cause different strengths of the genetic correlation when the correlations are based on plants originating from a single population or on pooled material from different populations.

The low genetic correlations between plant growth characters and growth rhythm characters are striking. Owing to the errors in the estimates, however, far reaching conclusions cannot be drawn. May be that the same genes are not responsible for characters of growth rhythm and plant growth, or that additive gene action plays a lesser role for plant growth than for growth rhythm.

A comparison between the phenotypic and genotypic correlations shows that the interpretation would not be the same when using the phenotypic correlations only. This in turn calls for more studies on genetic correlation between characters of economic importance.

Between-year correlations of the same character

Usually these types of correlation are based on phenotypic values. We have also carried out such correlations. However, we found it worthwhile to carry out a genetic correlation between the observations of the four different years. The calculation was done in the same way as for the genetic correlations between different characters. Thus, we assumed that D300 studied in 1981 and 1982 constituted two separate characters. This is not a nonsensical assumption since it may very well be assumed that different genes operate during different phases of the development. For example, the continuous decrease of the free growth from the first growth season to its disappearance during the sixth growth season might be explained in that way. The genetic correlations of the same character studied over several years might therefore give us some idea about which genes operate when.

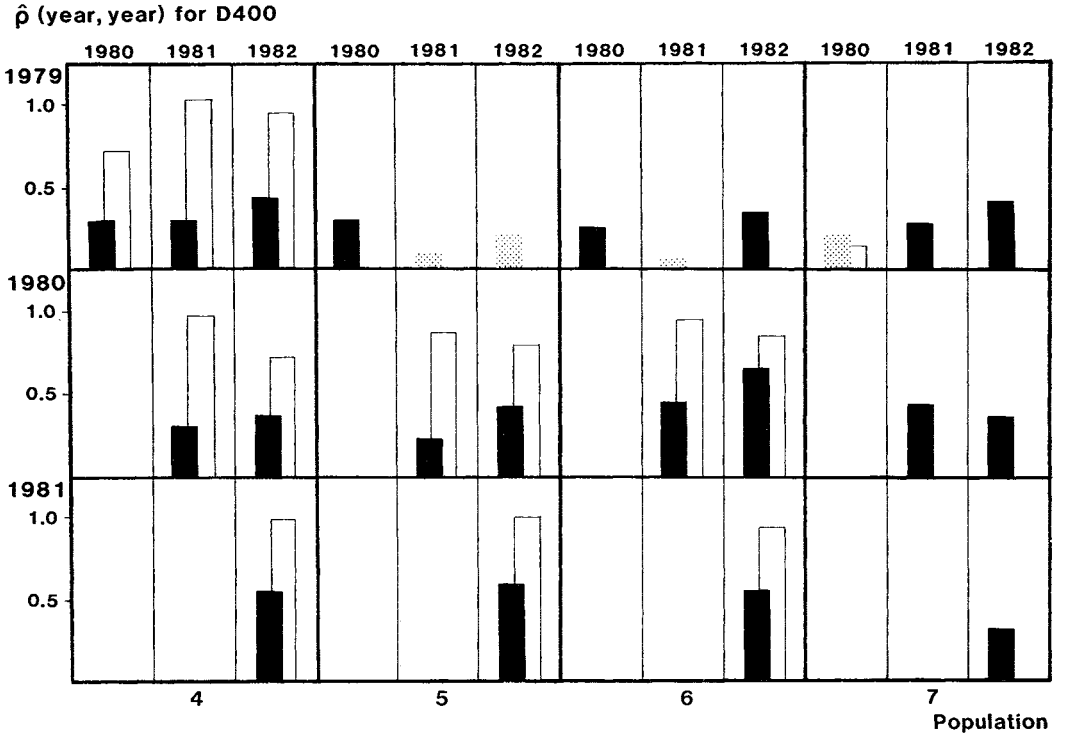
The correlations between years are only meaningful when there is a significant genetic variation for the character studied. Since this was not the case for many of the characters studied during 1979 we mainly have to base our results on the three last years of observation. This is probably too few years to detect any trends as outlined above. However, we have presented this technique and suggest that it may be used in related studies especially when data have been recorded over a longer time period than was the case in our study.

For the bud-flushing characters the genetic correlations were mostly high for populations 4–6 suggesting that the same genes are operating during the four years studied.

The relatively low correlations obtained for bud-set stage 710 for populations 6 and 7 (Fig. 5, bottom) suggest that different genes were operating in 1980 on the one hand and 1981–1982 on the other hand. The correlations for the attainment of 80% growth support this observation.

Unfortunately few meaningful genetic correlations for any of the two plant growth characters could be obtained.

The phenotypic correlations were always lower than the genetic ones (cf. Fig. 5). However, the difference between the two were not consistant. Thus, the phenotypic correlations do not always reflect the genetic component of the correlation.



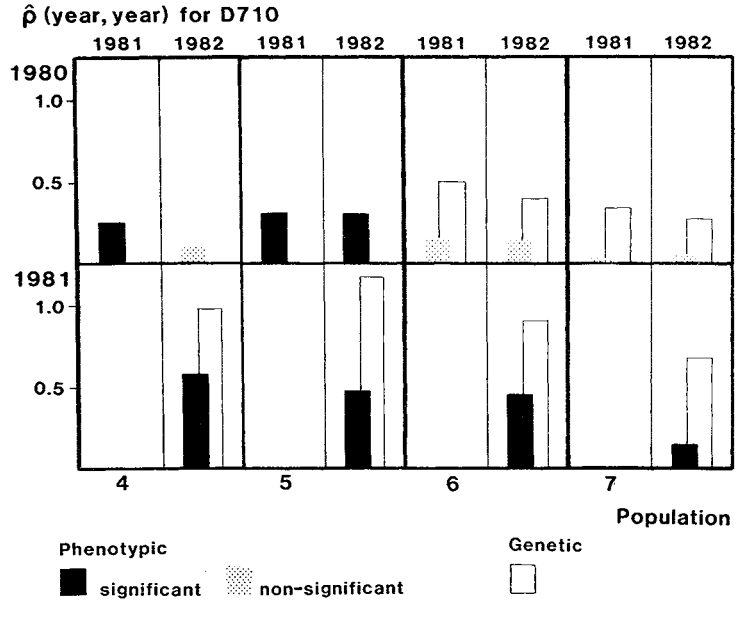


Fig. 5. The genetic and phenotypic correlations for attainment of bud-flushing stage D400 and bud-set stage D710.

References

Campbell, R.K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology 60*, 1036–1050.

Dietrichson, J. 1969*a*. Genetic variation of cold damage, growth rhythm and height growth in 4-year-old black spruce (*Picea mariana* (Mill.) BSP). *Meddr norske SkogforsVes. 27*, 109–129.

Dietrichson, J. 1969*b*. Growth rhythm and yield as related to provenance, progeny and environment. In *FAO, IUFRO, FO-FTB-69-2/3, 2nd World Consultation on Forest Tree Breeding*, Washington 7–16 Aug. 1969.

Dietrichson, J. 1970. Geografisk variasjon hos *Pinus contorta* Dougl. En undersøkelse med sikte på treslagets bruk i Norge. *Meddr norske SkogforsVes. 28*, 111–140.

Dietrichson, J. 1971*a*. A summary of studies on genetic variation in forest trees grown in Scandinavia with special reference to the adaptation problem. *Meddr norske SkogforsVes. 29*, 21–59.

Dietrichson, J. 1971*b*. Arvelig variasjon i fjelledelgran (*Abies lasiocarpa* (Hook.) Nutt.). *Meddr norske SkogforsVes. 29*, 1–19.

Dhir, N.K. 1976. Stand, family, and site effects in Upper Ottawa Valley white spruce. In *Proc. 12th Lake States For. Tree Improv. Conf. USDA For. Serv. Gen. Tech. Rep.*, NC-26, 88–97.

Dormling, I. 1979. Influence of light intensity and temperature on photoperiodic response of Norway spruce provenances. In *Proc. IUFRO Norway Spruce Meeting S.2.03.11-S.2.02.11, Bucharest 1979*, 398–408.

Ekberg, I., Eriksson, G. & Hadders, G. 1982. Growth of intra- and interprovenance families of *Picea abies* (L.) Karst. *Silvae Genetica 31*, 160–167.

Engsjö, T. & Persson, A. 1978. Projekt 63310302—Klimatzonkarta för gran. *Forskningsverksamheten 1977*, Royal College of Forestry, Dept. For. Genet., Research Notes 26, 5–16.

Eriksson, G. 1982. Ecological genetics of conifers in Sweden. *Silva Fennica 16*, 149–156.

Eriksson, G., Andersson, S., Eiche, V., Ifver, J. & Persson, A. 1980. *Severity index and transfer effects on survival and volume production of* Pinus sylvestris *in northern Sweden* (Studia For. Suec. 156). 32 pp.

Eriksson, G., Ekberg, I., Dormling, I. & Matérn, B. 1978. Inheritance of bud-set and bud-flushing in *Picea abies* (L.) Karst. *Theor. Appl. Genet. 52*, 3–19.

Franklin, E.C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genetica 28*, 207–212.

Kempthorne, O. 1973. *An introduction to genetic statistics*. 2nd printing. The Iowa State University Press, Ames.

Krutzsch, P. 1973. *Norway spruce*. Development of buds (IUFRO S.2.02.11., Royal College of Forestry) Stockholm, Sweden. 5 pp.

Levins, R. 1963. Theory of fitness in a heterogenous environment. II. Developmental flexibility and niche selection. *Am. Naturalist 97*, 75–90.

Lindgren, D. & Eriksson, G. 1976. Plantskoleförsök (Nursery studies). *Granförädling (Breeding Norway spruce)*. Conf. at Röskär, Bogesund, Jan. 20–26 1976. Dept. of Forest Genetics, Swedish College of Forestry, Stockholm, Sweden, 57–71.

Lundkvist, K. 1979. Allozyme frequency distributions in four Swedish populations of Norway spruce (*Picea abies* K.). I. Estimation of genetic variation within and among populations, genetic linkage and a mating system parameter. *Hereditas 90*, 127–143.

Morgenstern, E.K. 1974. Open pollinated progeny testing in a black spruce breeding program. In *Proc. Northeastern Forest Tree Improvement Conference, State University of New York, Aug. 7–9 1974*. 8 pp.

Perttu, K. & Huszár, A. 1976. *Vegetationsperioder, temperatursummor och frostfrekvenser beräknade ur SMHI-DATA* (Royal College of Forestry, Dept. of Reforestation, Research Notes 72).

Pollard, D.F.W. & Ying, C.C. 1979*a*. Variance in flushing among and within stands of seedling white spruce. *Can. J. For. Res. 9*, 517–521.

Pollard, D.F.W. & Ying, C.C. 1979*b*. Variation in response to declining photoperiod among families and stands of white spruce in southeastern Ontario. *Can. J. For. Res. 9*, 443–448.

Rehfeldt, G.E. 1974*a*. *Genetic variation of Douglas-fir in the northern Rocky Mountains*. Intermt. For. & Range Exp. Sta., Ogden, Utah, USA. USDA For. Serv. Res. Note INT-184. 6 pp.

Rehfeldt, G.E. 1974*b*. Local differentiation of populations of Rocky Mountain Douglas-fir. *Can. J. For. Res. 4*, 399–406.

Rehfeldt, G.E. 1983. Genetic variability within Douglas-fir populations: Implications for tree improvement. *Silvae Genetica 32*, 9–14.

Skrøppa, T. 1982. Genetic variation in growth rhythm characteristics within and between natural populations of Norway spruce. A preliminary report. *Silva Fennica 16*, 160–167.

Ståhl, E.G. 1984. *Variation in shoot growth phenology among clones and populations of* Pinus sylvestris *L.* (Thesis. Swedish University of Agricultural Sciences, Dept. of Forest Yield Research). Garpenberg. 103 pp.

Wright, J.W. 1963. Genetic variation among 140 half-sib Scotch pine families derived from 9 stands. *Silvae Genetica 12*, 83–89.

Acknowledgements. This investigation was supported by a grant from the Forestry Society. The able assistance of Mr Lennart Norell, Mrs Ewa Winkler, Mr Kjell Lännerholm and Mrs Lena Glantz Erikson is gratefully acknowledged.