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Inheritance of Bud-Set and Bud-Flushing in *Picea Abies* (L.) *Karst*[*]

G. Eriksson, I. Ekberg, I. Dormling, B. Matérn

Department of Forest Genetics, the Phytotron and Department of Forest Biometry, Swedish University of Agricultural Sciences, Uppsala and Stockholm (Sweden)

D. von Wettstein

Department of Physiology, Carlsberg Laboratory, Copenhagen (Denmark)

Summary. Diallel crosses were made between clones of a French and a Swedish provenance of *Picea abies*. The former is characterized by a long critical night length for bud-set and a late flushing of the buds; the latter by a short critical night length for bud-set and an early flushing of the buds. The F_1 hybrid seedlings and their French and Swedish intraprovenance half-sibs were tested over three growth periods in the phytotron at the College of Forestry, Stockholm. In comparison with intraprovenance half-sibs, the hybrid progenies gave, on average, an intermediate response for the photoperiodic control over bud-set and for the temperature requirements for bud-flushing. This indicates the prevalence of additive action of multiple factors in the determination of the photoperiodic and temperature response. However, individual interprovenance hybrid progenies revealed a range of responses, and in certain combinations the response of these hybrids and their intraprovenance half-sibs coincided. By selection of suitable parents, interprovenance crosses can be used to produce hybrids with desired photoperiodic characteristics and temperature requirements.

Key words: Critical night length – Photoperiodism – Bud-flushing – Temperature requirements – Provenance crosses – General and specific combining ability – Breeding values

Introduction

Populations of many tree species from the temperate zone display distinct clinal patterns of variation in such photoperiodic responses as terminal bud formation, plants from northerly or high altitude regions being adapted to terminate height growth at shorter night lengths than plants from southerly or lowland regions (Sylvén 1940; Langlet 1943; Johnsson 1951 and 1977; Pauley and Perry 1954; Vaartaja 1959; Holzer 1966; Dormling et al. 1968; Morgenstern 1969; Håbjørg 1972; Magnesen 1972; Dormling 1973; Heide 1974; Holzer and Nather 1974).

The inheritance of the photoperiodic response is of interest both from a theoretical and practical point of view. How light-dark cycles regulate the activity of genes determining plant growth and development remains an unsolved problem. Knowledge about the inheritance of photoperiodically controlled characters is essential for successful combination breeding using two populations from different latitudes or altitudes. The knowledge acquired from crossing trees from different populations is believed to be of value for the future breeding of *Picea abies* in Sweden (Ekberg et al. 1976). In most regions of Sweden, frost hardiness is of importance for a successful reforestation. This means that bud-flushing and bud-set, as well as lignification and hardening, must take place at an appropriate time so as to avoid damage by late frosts in the spring and early frosts in the autumn.

The autochtonous populations of *Picea abies* in Sweden are characterized by an earlier onset of bud-flushing than eastern European populations (Eriksson et al. 1974). Bud-set also takes place earlier in the autochtonous Swedish populations than in eastern European ones (Dormling 1973). It is evident that a combination of the late bud-flushing of eastern European populations and the early bud-set of the autochtonous Swedish populations is highly desirable. To be of practical value however, such hybrids should also have a satisfactory growth capacity.

In Fig. 1 the percentage of plants which at a given night length sets buds is represented schematically for Swedish × Swedish and continental × continental progenies, respectively. The curve for a provenance hybrid may be found midway between the two parent families, close to one parent family or close to the other.

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[*] With gratitude and appreciation we dedicate this paper to Åke Gustafsson at the occasion of his 70th birthday, April 8, 1978

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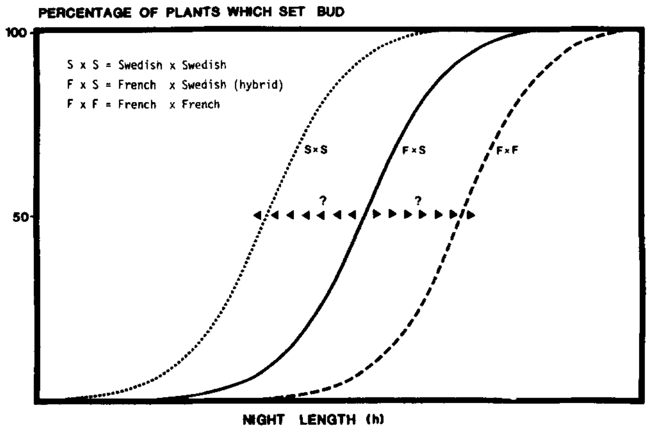


Fig. 1. Diagram illustrating the purpose of the present investigation. When the number of plants which set buds is plotted against the night length applied, the Swedish and French intraprovenance crosses yield separated curves. The position of the curve for hybrid plants from crosses involving the two provenances is analysed

The position of a hybrid curve will determine if a particular hybrid can yield a combination of the desired response in bud-flushing, bud-set and lignification. It is the purpose of this investigation to analyse the inheritance of the time for bud-flushing and bud-set in *Picea abies* hybrid plants from crosses between Swedish and continental provenances.

Material and Methods

The pattern of inheritance of bud-flushing and bud-set can be analysed through crosses between and within different provenance populations. In the springs of 1973 and 1974, clones originating from Lapland and France were flowering in a plantation at Bogesund, ten kilometres outside of Stockholm. The French clones had been selected from a stand established with plants obtained from seeds collected in Northern France. Their exact origin has not been possible to trace. From each of the two populations, four clones were selected to be included in a half diallel crossing scheme, i.e. reciprocal crosses were not carried out. Selfings were made but the resulting seeds have not yet been tested. Owing to limited flowering, five of the crosses did not produce the desired number of seeds.

Bud-set of the progenies was tested during three consecutive growth periods in the phytotron at the College of Forestry, Stockholm, whereas bud-flushing was studied only during the second and third growth period, also in the phytotron. Due to a space limitation, not all combinations could be tested simultaneously, but some of the crosses were tested twice, with a satisfactory repeatability of the results. Between growth periods, the plants were transplanted into larger pots, making necessary a reduction of the number of plants. Also, certain families had to be excluded from the test during the second and third growth period. The progenies studied and the number of plants per progeny are given in Table 1. The diallel schemes are presented with the discussion of the results.

The technique for testing the critical night length for bud-set (CN) was the same as that reported by us in a previous paper (Dormling et al. 1974). All plants were grown in continuous light for 11 weeks and thereafter distributed to different photoperiods with a night length ranging from 1 h 30 min to 7 h 45 min. The plants were kept for six weeks under these differing photoperiods. The derivation of the critical night length for the progeny of a cross was carried out as described in Fig. 2. For each replicate, the percentage of plants which had set bud was plotted against the night length. The number of hours at 50 per cent bud-set was read from the graphs and an average for the four replicates was calculated. It may be added that the progeny of Fig. 2 are used for illustration because of their wide variation between the replicates.

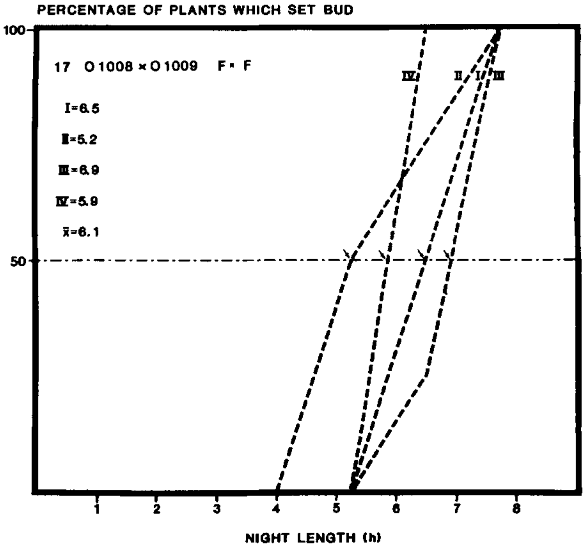


Fig. 2. Determination of the critical night length for bud-set among seedling progenies of *Picea abies* resulting from the cross 0 1008 X 0 1009. The percentages of bud-set in the four replicates are plotted against night length. The critical night length in hours is determined as the value giving 50% bud-set and is indicated by the arrows

The technique used to study bud-set was modified during the second and third growth period when the mean days to bud-set were determined. Following bud maturation and breakage of bud dormancy (see below), all plants were grown in continuous light. After one week, all plants were exposed to one hour of darkness per day. For every week thereafter, the night length was increased by one hour per week, all plants being exposed to the same conditions. Useful results were obtained with a number of plants that were only one fourth of the number used in the earlier experiment. This technique was pretested on a limited number of families during the first growth period. However, in this case, the exposure to one hour of darkness per day was not started until 10 weeks after sowing.

Bud maturation occurred for 8 weeks at 20° C-16 hours darkness. Conditions applied to break bud dormancy were: 1 week at 10° C-16 hours darkness; 1 week at 5° C-16 hours darkness; 1 week at 2° C-24 hours darkness; 1 week at 10° C-16 hours darkness. Thereafter the plants were moved into 20° C-continuous light.

The stages of bud-break were classified according to the scheme published by Krutzsch (1973):

0. Dormant buds
1. Buds slightly swollen, needles below buds bent backwards and outwards
2. Buds swollen, green to grey-green in colour, bud scales still closed

Table 1. List of progenies from the different provenance crosses and number of plants tested during the first to third growth period
CN = Determination of critical night length for bud-set

Crosses		Number of plants			
		Growth period			
		First		Second	Third
Progeny Number	French X French	CN	Bud-set	Bud-set and flushing	Bud-set and flushing
2	0 1006 X 0 1008	80	–	–	–
3	0 1006 X 0 1009	80	–	–	–
4	0 1007 X 0 1006	80	–	–	–
16	0 1007 X 0 1008	48	–	–	–
17	0 1008 X 0 1009	112	16	16	12
22	0 1009 X 0 1007	64	–	16	12
	Swedish X Swedish				
23	AC 1008 X AC 2040	64	–	16	12
24	AC 1008 X AC 3004	64	16	16	12
25	AC 1009 X AC 1008	64	–	16	12
26	AC 1009 X AC 2040	64	–	16	12
27	AC 2040 X AC 3004	64	–	16	–
28	AC 3004 X AC 1009	64	–	16	12
	Hybrids				
29	AC 1008 X 0 1006	64	–	16	–
30	AC 1008 X 0 1007	64	–	16	12
31	AC 3004 X 0 1008	64	16	16	12
32	AC 3004 X 0 1009	64	16	16	12
33	0 1006 X AC 2040	64	–	16	–
34	0 1007 X AC 2040	64	–	16	–
35	0 1007 X AC 3004	64	–	16	12
11	0 1008 X AC 1008	192	16	16	12
36	0 1008 X AC 1009	64	–	16	12
37	0 1009 X AC 1008	64	16	16	12
38	0 1009 X AC 1009	64	–	16	12

3. Burst of bud scales, tips of needles emerging
4. First elongation of needles to about double bud length
5. First spread of needles, but have now the appearance of a painter's brush
6. Elongation of shoot, basal needles not yet spread
7. Differentiation of shoot, basal needles spread
8. All needles more or less spread, new buds developing

Throughout the experiment four replicates were used. During the first two growth periods, four plants per plot were used. Economic reasons necessitated a reduction of the number of plants per plot to three during the third growth period.

Results and Discussion

Bud-Set During the 1st Growth Period

The critical night length for individual progenies is shown in Figure 3. The critical night length for the progenies from crosses among the French trees varied between 5.3 and 6.1 hours; among the crosses of the Swedish trees, between 3.3 and 4.1 hours and from the French times Swedish crosses, between 4.2 and 5.0 hours. There is no overlapping between the three categories of progeny (Fig. 4) although the differences in critical night length between certain individual families from two different categories is small.

A small half diallel scheme (Fig. 5) comprised of two parents from each provenance was used to test a modified technique for determination of the mean days to bud-set. As mentioned above, the plants were grown in continuous light for 10 weeks and then one hour of darkness per day was added each week.

As illustrated in Fig. 5, the interprovenance hybrids are easily distinguished from the two intraprovenance hybrid progenies. These results should be compared to the ones obtained for the same families in the experiment for estimation of the critical night length shown in Figure 6.

♀ \ ♂	0 1006	0 1007	0 1008	0 1009	AC 1008	AC 1009	AC 2040	AC 3004
0 1006	-	R	5.8	5.7	R	-	4.2	-
0 1007	5.3	-	6.0	R	R	-	4.4	4.3
0 1008	R	R	-	6.1	4.9	4.2	-	R
0 1009	R	5.4	R	-	5.0	4.4	-	R
AC 1008	4.7	5.0	R	R	-	R	3.9	4.1
AC 1009	-	-	R	R	3.7	-	3.3	R
AC 2040	R	R	-	-	R	R	-	3.9
AC 3004	-	R	4.9	4.7	R	4.0	R	-

R = reciprocal cross tested

Fig. 3. The critical night length for bud-set in hours obtained for progenies in a diallel cross (R = reciprocal cross tested)

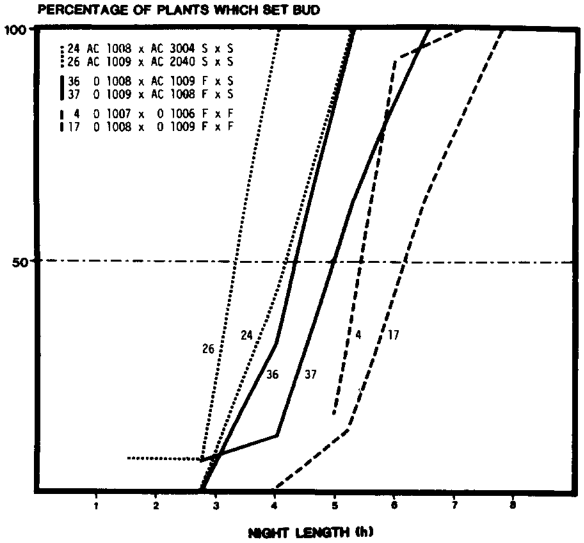


Fig. 4. Critical night length curves for bud-set of seedling progenies of *Picea abies* resulting from crosses within French (F X F), within Swedish (S X S) and between French and Swedish (F X S) provenances. For each type of the cross the progeny with the shortest and longest critical night length is shown

Qualitatively a good agreement is observed between the curves obtained in the two different ways (Figs. 5-6).

Thus, the interprovenance hybrids have in both cases moved slightly to the left of the arithmic mean between the two intraprovenance hybrid curves. This suggests that it might be possible to derive the critical night length from diagrams of the type shown in Figure 5. However, these diagrams cannot be used directly to determine the critical night length since the bud-set is the result of a process of development which had been initiated two to four weeks earlier.

Holzer and Nather (1974) used yet another technique to characterize populations by their photoperiodic response for bud-set. These authors determined at regular intervals the percentage of plants which had set bud and added these percentages to a sum called 'Knospenzahl'. We made a similar calculation in Table 2 for the data presented in Figure 5. The mean value of the 'Knospenzahl' for the interprovenance hybrids is much closer to the 'Swedish x Swedish family than to the 'French x French' family. The interpretation of the results is thus dependent on the technique used to evaluate the data. In the 'Knospenzahl' method it is inherent that the relations between the families change depending, for example, on how long the experiment is continued.

Bud-Set During the 2nd and 3rd Growth Period

The families studied in these two growth periods are shown in the diallel scheme of Figure 9. They can be split up into four small half-diallel mating designs (I-IV, Fig. 10) which are used to illustrate the data obtained for

Table 2. Calculation of 'Knospenzahl' according to the method of Holzer and Nather (1974)

Cross			Percentage of plants which set bud on day							'Knospenzahl'
			22	29	36	43	50	57	64	
24	AC 1008 X AC 3004	S X S	0	6	6	62	100	100	100	374
11	0 1008 X AC 1008	F X S	0	12	12	25	75	88	100	312
31	AC 3004 X 0 1008	S X F	0	0	0	19	88	94	100	301
32	AC 3004 X 0 1009	S X F	0	0	0	44	69	100	100	313
37	0 1009 X AC 1008	F X S	0	0	0	40	64	81	100	285
17	0 1008 X 0 1009	F X F	0	0	0	0	12	23	100	135

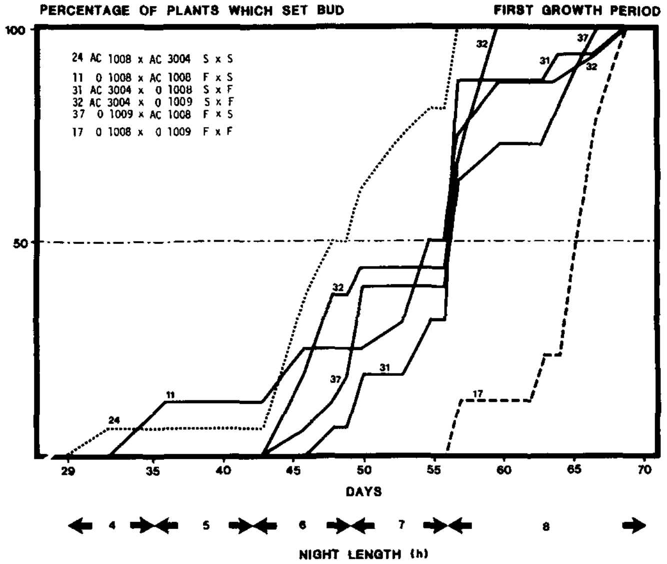


Fig. 5

Fig. 5-8. Bud-set of the seedling progenies from the crosses between and within French and Swedish provenances in the small diallel cross No. I (cf. Fig. 10)

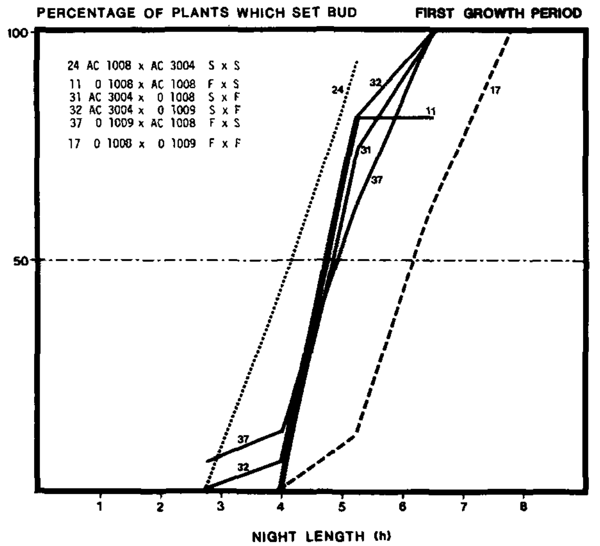


Fig. 6

these two growth periods. Some of the families are of course common to two or three of the half-diallels.

The results from the 2nd and 3rd growth periods for the half-diallel (I) are given in Figures 7 and 8. The interprovenance hybrids are intermediate to the intraprovenance parent combinations. In contrast to the situation during the first growth period (Figs. 5, 6), the interprovenance hybrids have moved slightly towards the direction of the curves for the F x F cross.

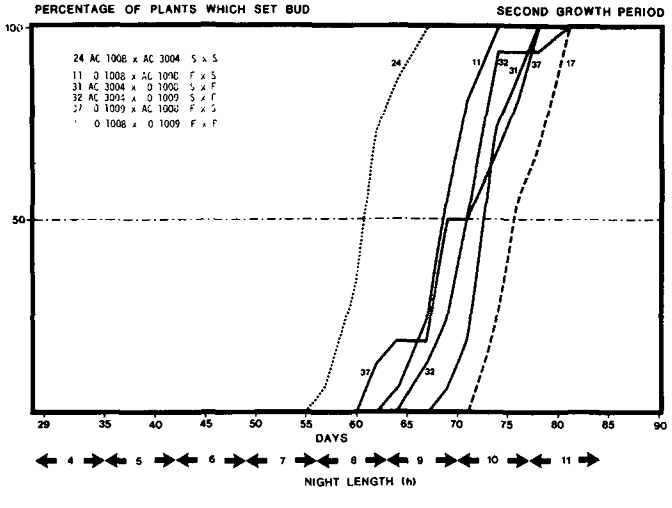


Fig. 7

Fig. 5. First growth period; bud-set after successively increased night length. Fig. 6. First growth period: critical night lengths. Figs. 7,8. Second and third growth period; bud-set after successively increased night length

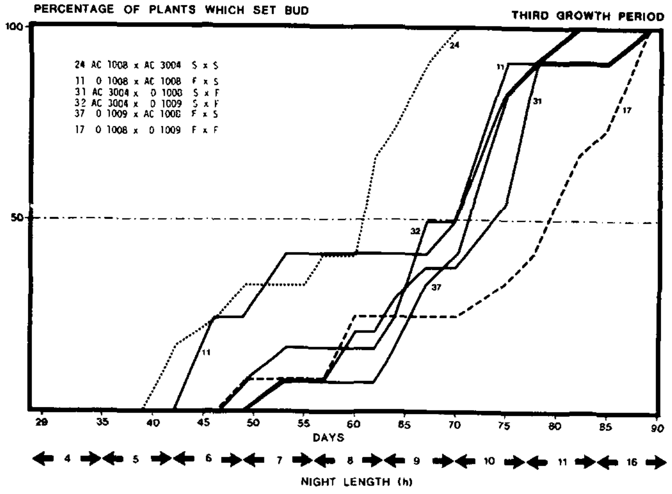


Fig. 8

The hybrids of half-diallel II exhibit an interesting development from the first to the third growth period (Figs. 11-13). There is a pairwise separation of the four interprovenance hybrids which becomes more pronounced by age. In the 3rd growth period, two of the progenies display a photoperiodic response close to the S x S progeny and two towards the F x F progeny. The same trend is apparent for half-diallel III (Figs. 14-16). This pairwise separation can be attributed to the breeding values of the

♂ ♀	0 1007	0 1008	0 1009	AC 1008	AC 1009	AC 3004
0 1007	-	-	R	R	-	35
0 1008	-	-	17	11	36	R
0 1009	22	R	-	37	38	R
AC 1008	30	R	R	-	R	24
AC 1009	-	R	R	25	-	R
AC 3004	R	31	32	R	28	-

Fig. 9. The diallel cross involving six parents studied during the second and third growth period (11-38 = identification numbers of the crosses; R = reciprocal cross tested)

clones rather than to the existence of a high specific combining ability (Fig. 33 and following subsection). In half-diallel IV, the interprovenance hybrids react intermediately to the intraprovenance parent combinations (Figs. 17-19). If the values of the progenies resulting from crosses among the three Swedish trees in the half-diallel comprising six clones (Fig. 9) are combined with those from the crosses among the three French trees, an increasingly greater difference is observed from the first to the third growth period for the photoperiodic response (Figs. 20-22). On an average, the curves for the interprovenance hybrids are located close to a curve constructed on the arithmic mean between the intraprovenance curves.

Flushing During the 2nd and 3rd Growth Period

The results from the studies of the bud and shoot development during the second and third growth periods are presented graphically in the same way as the results for the bud-set observation (Figs. 23-32). During the second growth period, the progenies of the Swedish intraprovenance crosses flushed about three days earlier than their French counterparts. During the third growth period, the difference was about 6 days. An examination of the curves for the individual progenies of the four half-diallels revealed an overlapping between the interprovenance hybrids and the F x F curves during the 2nd growth period. This is also clearly seen from Figure 31, in which the pooled average data are shown. In contrast to this situation, an overlapping occurred only once (Fig. 30) during the 3rd growth period. The temperature conditions were in both cases the same, as were the conditions during the resting period between the growth periods. However, the conditions during the preceding growth period could have affected the bud-flushing.

I

♂ ♀	0 1008	0 1009	AC 1008	AC 3004
0 1008	-	17	11	R
0 1009	R	-	37	R
AC 1008	R	R	-	24
AC 3004	31	32	R	-

II

♂ ♀	0 1008	0 1009	AC 1008	AC 1009
0 1008	-	17	11	36
0 1009	R	-	37	38
AC 1008	R	R	-	R
AC 1009	R	R	25	-

III

♂ ♀	0 1008	0 1009	AC 1009	AC 3004
0 1008	-	17	36	R
0 1009	R	-	38	R
AC 1009	R	R	-	R
AC 3004	31	32	28	-

IV

♂ ♀	0 1007	0 1009	AC 1008	AC 3004
0 1007	-	R	R	35
0 1009	22	-	37	R
AC 1008	30	R	-	24
AC 3004	R	32	R	-

11-38 = identification numbers of the crosses
R = reciprocal cross tested

Fig. 10. The four subsets of diallel crosses analysed during the second and third growth period

An increasing differentiation between the three types of progeny with increasing age, noted for the bud-set, is also apparent for the start of a new growing season (compare Figs. 31 and 32).

Analysis of Variance

In order to be able to judge the possibilities for a successful breeding program based on inter- and intraprovenance crosses, we should know the size of the variation in the general combining ability (GCA) of the clones and the specific combining ability (SCA). The latter should perhaps be called more appropriately, the non-additive variation. In the present investigation it is also of interest to know, for both the general and specific combining ability, how much of the variation is attributable to differences between the provenances and how much reflects 'within provenance' effects.

The critical night length for bud-set for each plot, i.e. for each cross in each block, was determined graphically from diagrams of the type shown in Figure 2. The principle for calculating mean days to bud-set for each cross is illustrated in Table 3. The mean days for reaching the bud-stages 3, 4.5 and 6 were determined graphically for each plot from diagrams showing the bud-flushing of each cross in each block (e.g. Fig. 24). The analysis of variance is based on these plot means.

The literature on diallel and partial diallel experiments is almost exclusively confined to cases in which the par-

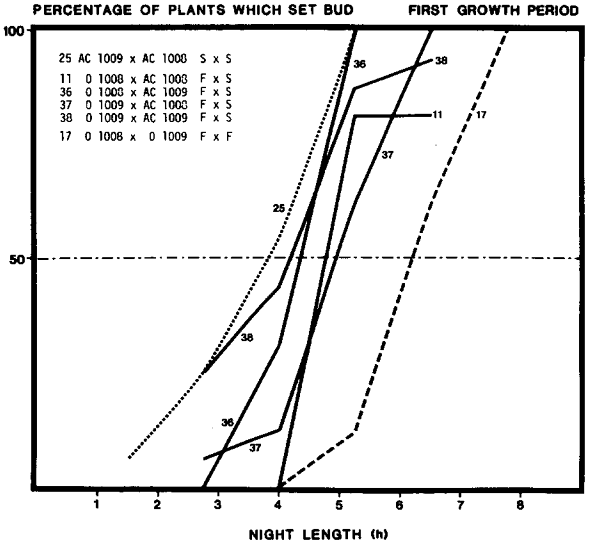


Fig. 11

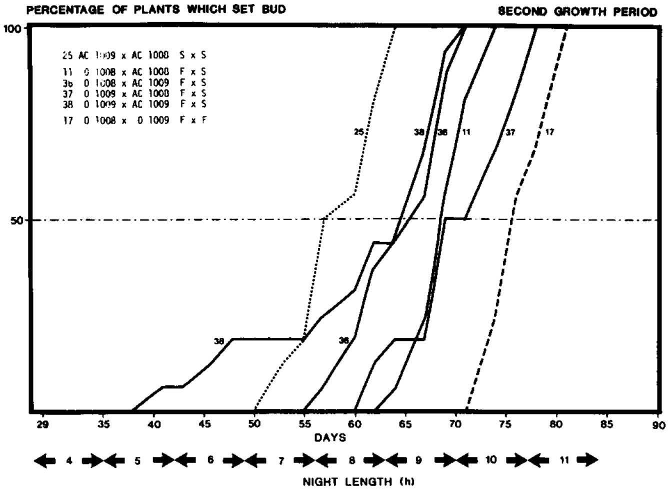
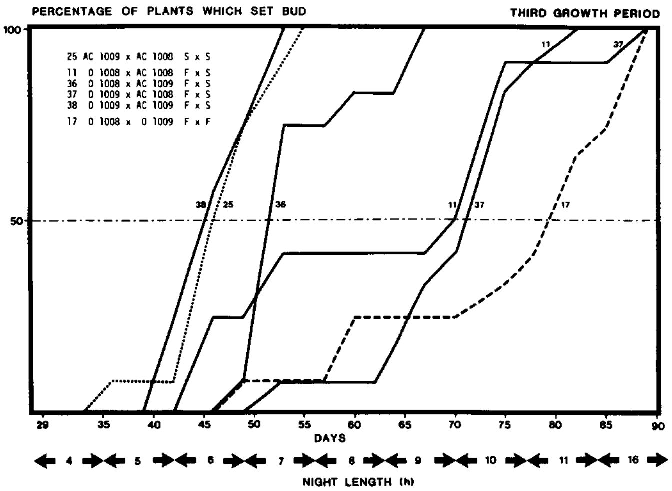


Fig. 12

Figs. 11, 13. Bud-set in seedling progenies from the small diallel cross II (cf. Fig. 10)

Fig. 11. First growth period; critical night lengths



Figs. 12, 13. Second and third growth period; bud-set after successively increased night length

Fig. 13

Table 3. The method of calculating mean days to bud-set. This was made for each block separately

Day of record	43		46		48		50		53		55		57		60		62		64		67
Mean days between two records		44.5		47		49		51.5		54		56		58.5		61		63		65.5	
Proportion of plants which set buds	0		$\frac{1}{16}$		0		0		0		0		$\frac{1}{16}$		$\frac{3}{16}$		$\frac{5}{16}$		$\frac{4}{16}$		$\frac{2}{16}$

Mean days to bud-set: $\frac{44.5}{16} + \frac{56}{16} + \frac{58.5 \times 3}{16} + \frac{61 \times 5}{16} + \frac{63 \times 4}{16} + \frac{65.5 \times 2}{16} = 60.25$

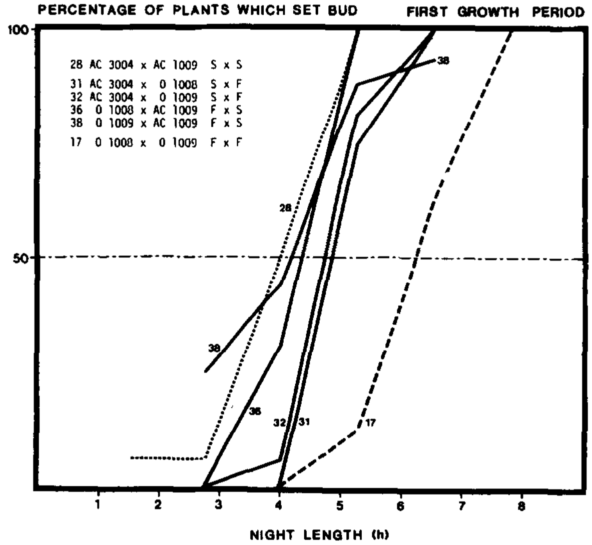


Fig. 14

Figs. 14-16. Bud-set in seedling progenies from the small diallel cross III (cf. Fig. 10). **Fig. 14.** First growth period; critical night lengths

ents or the lines tested constitute one homogeneous group.

However, Hinkelmann (1974) studied a case in which there are m groups, each represented by n trees, and where all n^2 crosses between members of two different groups were carried out. The analysis presented in this paper cannot be used in the present very inbalanced situation. One further reason is that Hinkelmann assumed that there were no crosses within groups. However, we shall try to follow his notation for the general combining ability and specific combining ability at the two levels, provenances and individuals within a provenance.

Mathematical Model

The design is an incomplete diallel laid out in r (= 4) randomised blocks. The number of parents is denoted n (n = 8 in the data from the first growth period; n = 6 in the data from the second and third growth period). There are n/2 parents from each one of the two provenances. The total number of crosses are called N (N = 23 in the first; N = 13 in the second and third periods). Let the parents be numbered 1, 2, ..., n. Assume that data are available for the cross between parents i and j, and that these parents are from provenances u and v, respectively. (Here u, and v, assume only the values 1 and 2, standing for French and Swedish provenance, respectively). Let further u_{ijk} be the value of a quantitative character observed in the kth replication of this cross (k = 1, 2, 3, 4).

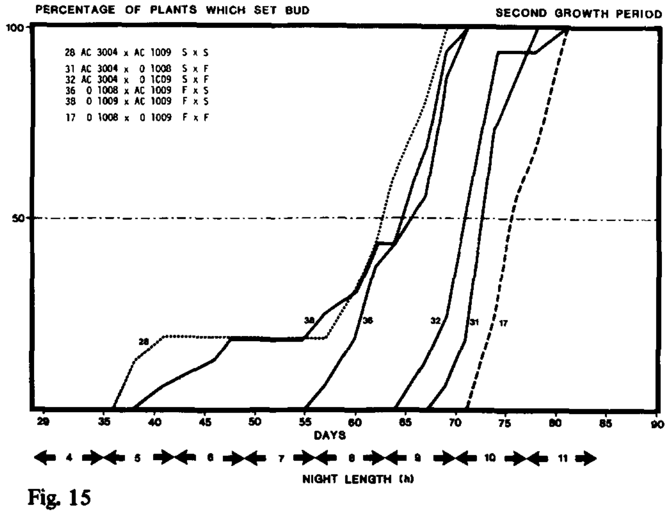


Fig. 15

Figs. 15, 16. Second and third growth period; bud-set after successively increased night length

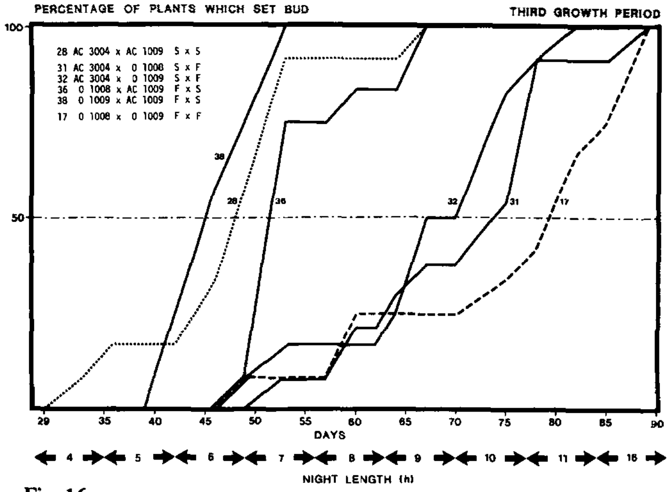


Fig. 16

We then write

$$y_{ijk} = \mu + G_u + G_v + S_{uv} + g_i + g_j + s_{ij} + b_k + \epsilon_{ijk} \qquad (1)$$

where

μ = an effect common to all blocks and crosses
G_u = the average GCA of provenance u
S_{uv} = the average SCA in the cross between parents from provenances u and v
g_i = the GCA of parent i
s_{ij} = the SCA in the cross between parents i and j
b_k = the effect of block k
ϵ_{ijk} = an error due to the randomisation within a block, observational error, within-family variation, etc.

The symbols, except the general mean (μ), represent deviations from means of the next higher order. Thus, g_i denotes a deviation from the average G_u of the corresponding provenance; G_u represents a deviation from μ, etc.

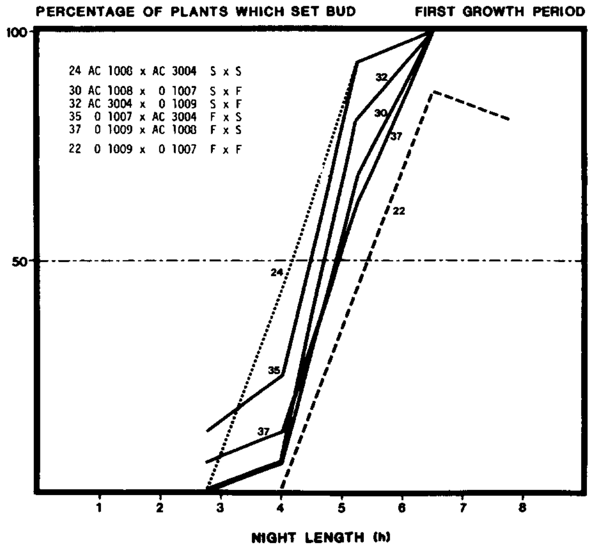


Fig. 17

Figs. 17-19. Bud-set in seedling progenies from the small diallel cross IV (cf. Fig. 10). Fig. 17. First growth period; critical night lengths

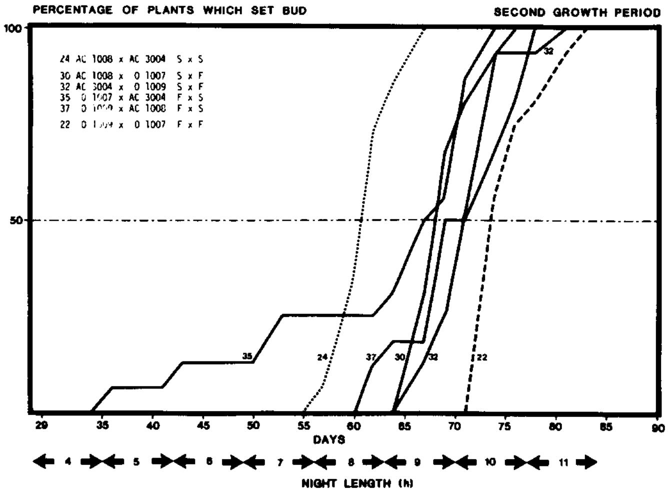


Fig. 18

Figs. 18, 19. Second and third growth period; bud-set after successively increased night length

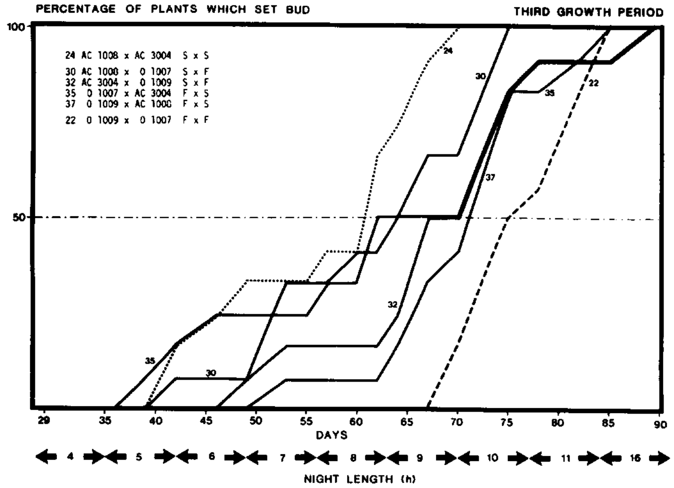


Fig. 19

We assume that the parents can be considered as a random sample from the respective population (= provenance). Hence, $\{g_i\}$ and $\{s_{ij}\}$ are supposed to be observations of random variables with means O and variances σ_g^2 and σ_s^2, respectively. Similarly, the error term (ϵ_{ijk}) is assumed to vary stochastically around O with variance σ_ϵ^2. It is evidently not reasonable to make any statistical assumptions about $\{G_u\}$ and $\{S_{uv}\}$. We consider them as (unknown) constants.

Computational Methods

We want to test some hypotheses concerning the values of the parameters $\{G_u\}$, $\{S_{uv}\}$, $\{g_i\}$ and $\{s_{ij}\}$, and also to compute estimates of the components of variance, σ_g^2 and σ_s^2. For this purpose we carry through an analysis of variance (ANOVA).

Owing to the structure of the data, the analysis is performed by a combination of the classical ANOVA method of summing squares in different subsets and the method of fitting constants. To describe the computations, we introduce certain sums of squares. Three sums of squares (Q_1, Q_2, and Q_3) are computed as in an ordinary ANOVA of an experiment with N treatments (= crosses) in r randomised blocks. They are presented in part a) of Table 4, together with the corresponding degrees of freedom (the sum for blocks, Q_2, is included here for completeness, it has not been used in the calculations reported below.). Four sums of squares (Q_4, Q_5, Q_6, Q_7) have been computed by smoothing the means $\{y_{i.j}\}$ of the N families by linear forms in some of the combining abilities of the expression (1). the minimised sums are multiplied by r to fit in with the computation of Q_1, Q_2, and Q_3, which is based on the plot value as unit. The graduating linear expressions and the degrees of freedom are given in part b) of Table 4.

Table 5 shows how the sums of squares that are related to the variation among specific subsets of the parameters of (1) have been obtained from Q_1, ..., Q_7. By dividing these sums by their degrees of freedom, the mean squares used in the variance-ratio tests are obtained. The estimation of the variance components (σ_g^2, σ_s^2 and σ_ϵ^2) is performed by equating the sums of squares of the table by their expected values. If this leads to a negative estimate it is replaced by zero. The expectations can usually be obtained by straight forward methods. The only complicated expression involved seems to be the expectation of Q_5. To show this value we need some additional notation. Let the

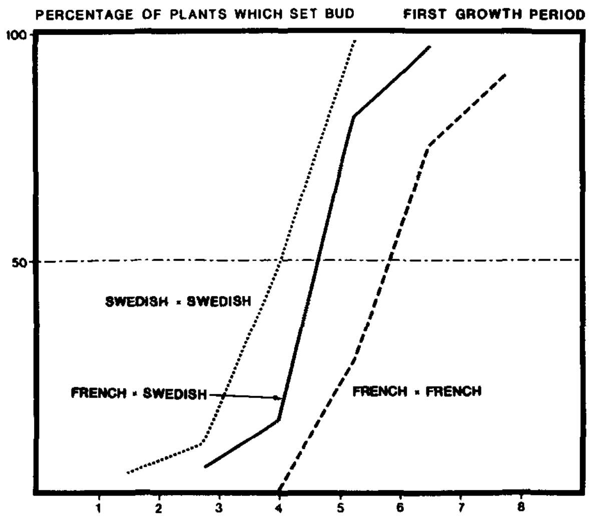


Fig. 20

Figs. 20-22. Average curves for the percentage of bud-set in the seedling progenies from crosses between and within French and Swedish provenances in the diallel cross shown in Fig. 9 during the first, second and third growth period. In Figs. 21 and 22 the inter-provenance curve is compared to the arithmetic mean of the intra-provenance curves obtained by plotting the mean at intervals of 10 per cent bud-set

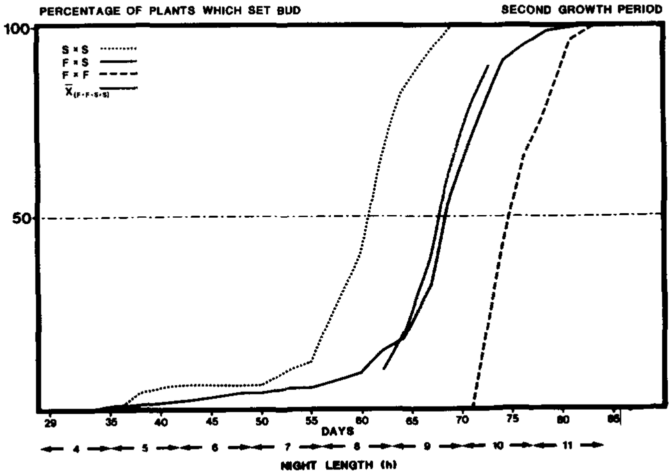


Fig. 21

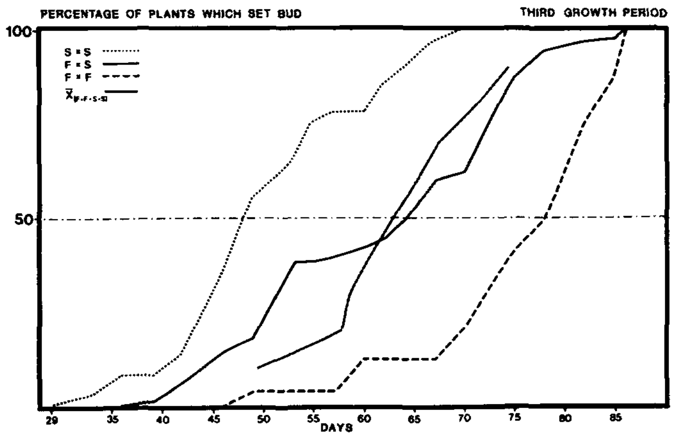


Fig. 22

Table 4. Sums of squares used in the analysis of variance

a) Sums computed as in ANOVA of randomised blocks

Source of variation	Notation for the sum of squares	Degrees of freedom
Crosses	Q_1	N-1
Blocks	Q_2	r-1
Errors	Q_3	(N-1) (r-1)

b) Sums based on graduating linear expressions

Linear expression	Notation for the sum of squares	Degrees of freedom
$\mu+G_u+G_v$	Q_4	N-2
$\mu+G_u+G_v+S_{uv}$	Q_5	N-3
$\mu+G_u+G_v+g_i+g_j$	Q_6	N-n
$\mu+G_u+G_v+S_{uv}+g_i+g_j$	Q_7	N-n-1

Table 5. Analysis of variance: Sums of squares used in variance-ratio test and in estimating variance components. The symbols $Q_1, \dots, Q_7$ are explained in Table 4

Source of variation	Sum of squares	Degrees of freedom
GCA between provenances (G_u)	Q_1-Q_4	1
GCA within provenances (G_i)	Q_5-Q_7	n-2
SCA between provenances (S_{uv})	Q_6-Q_7	1
SCA within provenances (s_{ij})	Q_7	N-n-1
Error (ϵ)	Q_3	(N-1) (r-1)

j:th parent be involved in N_{1j} crosses in the group French × French; in the N_{2j} crosses in the group Swedish × Swedish and N_{3j} crosses in the group Swedish × French. Evidently one of the numbers N_{1j} and N_{2j} must vanish. Let the total number of crosses in the three groups be N_1, N_2, and N_3. Thus $N_1 + N_2 + N_3 = 2N$. The expectation of Q_5 is

$$r\left(2N - \frac{N_{11}^2 + \dots + N_{1n}^2}{N_1} - \frac{N_{21}^2 + \dots + N_{2n}^2}{N_2} - \frac{N_{31}^2 + \dots + N_{3n}^2}{N_3}\right)\sigma_g^2 + r(N-3)\sigma_s^2 + (N-3)\sigma_\epsilon^2 .$$

For comparison, variance components have also been estimated without regard to the provenances, i.e., as if the following simple model was appliable:

$$y_{ijk} = \mu + g_i + g_j + s_{ij} + b_k + \epsilon_{ijk} \qquad (2)$$

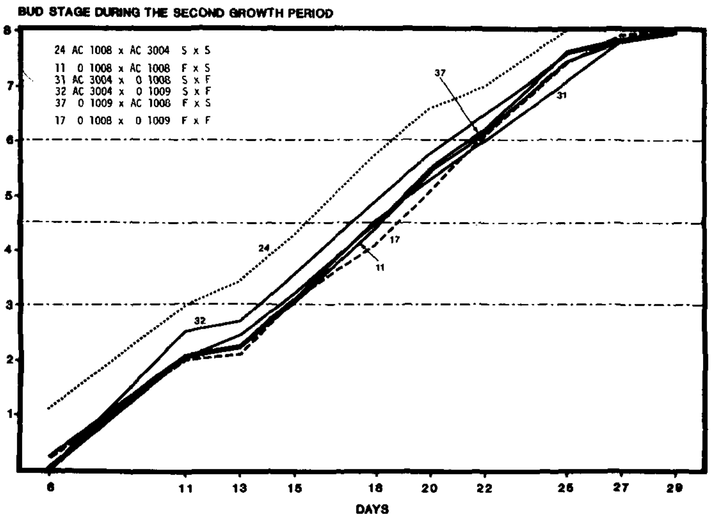


Fig. 23

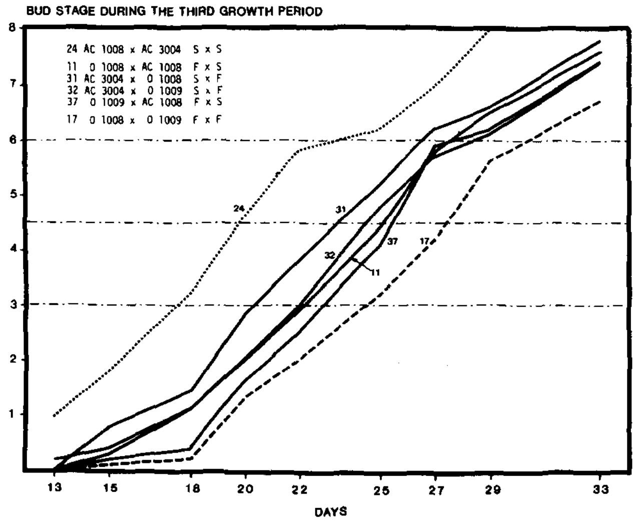


Fig. 24

Figs. 23-30. Bud-flushing during the second and third growth period among seedling progenies from the small diallel crosses No. I to IV of Fig. 10

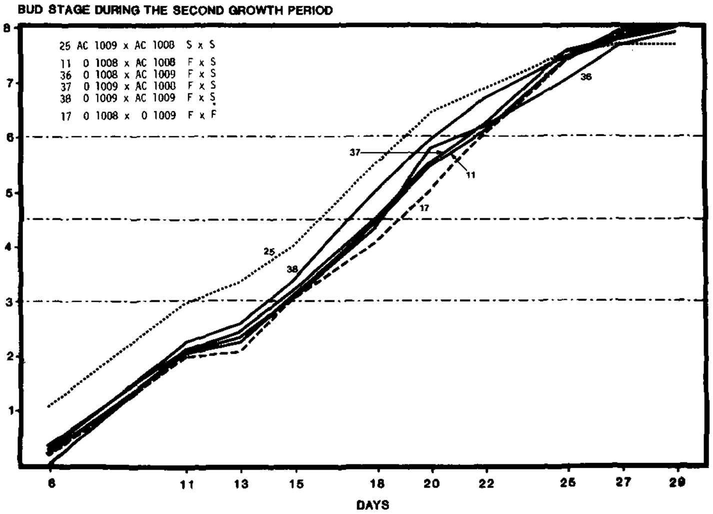


Fig. 25

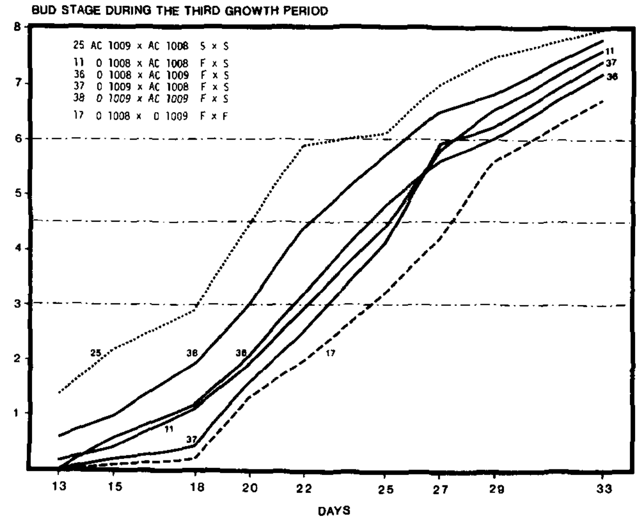


Fig. 26

General and Specific Combining Ability

For testing the occurrence of general and specific combining abilities we have computed a number of variance-ratios for Table 6. Estimates of variance are given in Table 7.

Since the number of parents tested is small (8 in the first; and 6 in the second and third periods), one can only expect strong effects to produce significance. It is therefore probable that the GCA's differ considerably between parents. This seems, to a large extent, to be due to a difference between the two provenances since 'GCA between' is in most cases significantly greater than the 'GCA within'. However, in four cases there is also a strong significance (at the 0.1 per cent level) for the ratio GCA within/Error. By multiplying the numbers of the first two columns, one finds that the 'GCA between' is in all cases significantly larger (at the 0.1 per cent level) than the error mean square. Owing to the small number of parents one should perhaps not attach too much importance to the observed differences between the ratios appertaining to different characters.

Passing to the specific combining ability, one finds that by multiplying the last two columns of Table 6 the 'SCA between' is significantly larger than the error terms for both critical night length (at the 1 per cent level) and

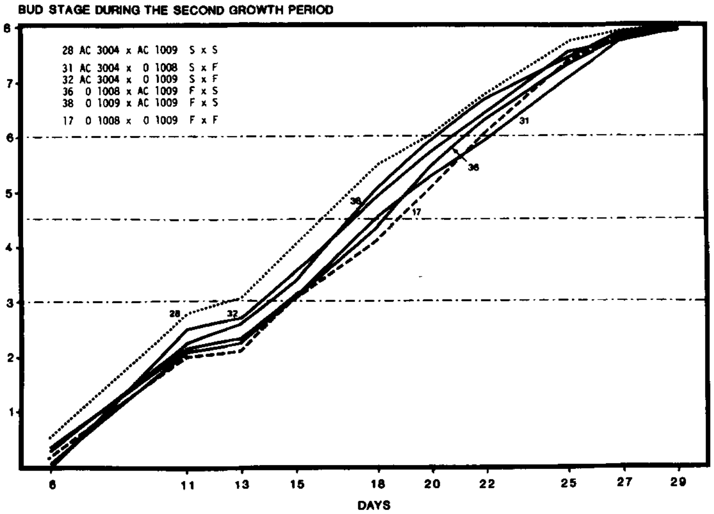


Fig. 27

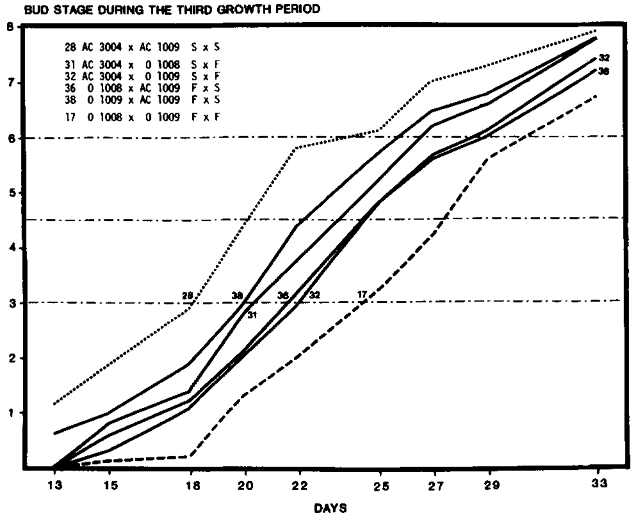


Fig. 28

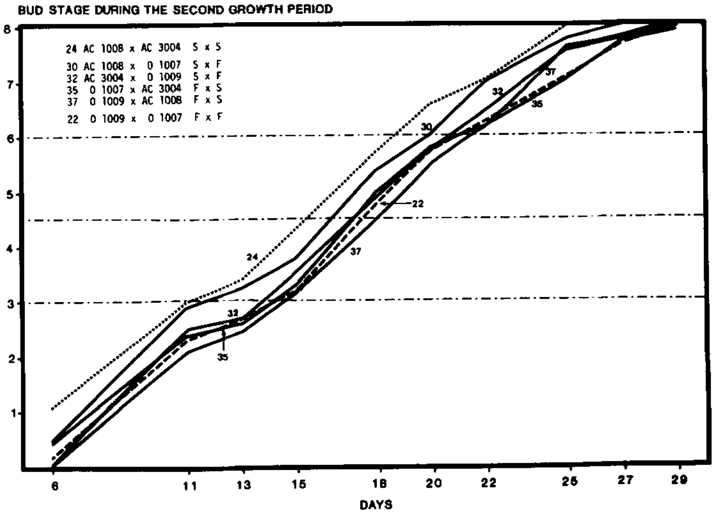


Fig. 29

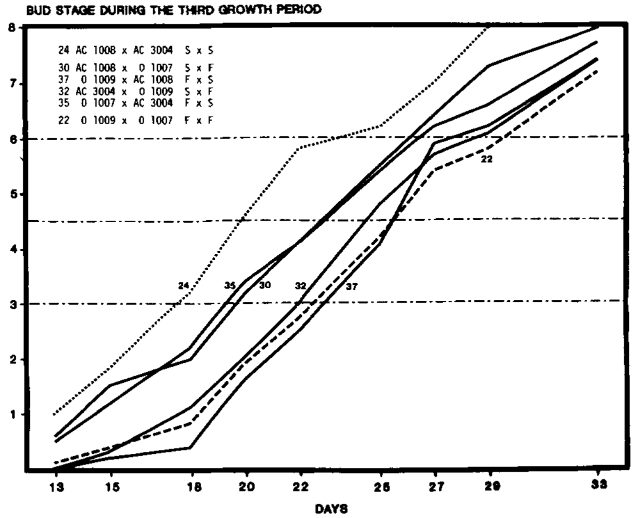


Fig. 30

bud-stage 6 in the 3rd period (at the 5 per cent level). The 'SCA within' is significantly larger than the error term in five cases (bud-set and bud-stage 3 in the 2nd growth period and bud-set and bud-stages 3 and 4.5 in the 3rd growth period).

The estimated components of variance, see Table 7 confirm the impression one gets from Table 6 of a predominantly additive gene action. When the components are estimated without regard to provenances, the estimated σ^2_g is larger than the estimated σ^2_s in all cases. When both components are estimated 'within provenances', this applies only in three of the nine characters. The explanation seems to be that the main part of the additive effect is the variation between provenances, as seen when comparing the first two columns of Table 7. With the exception of one character (critical night length), there is no indication of a corresponding provenance component of the specific combining ability.

Comparing the three growth periods, no fundamental differences in variance ratios or in estimated components of variance were found.

The results obtained by Tho (1977) also indicate that the winter bud formation in *Picea abies* is predominantly under additive control. He analysed diallel crosses, including reciprocals and selfings, between trees within three stands. The analysis was based on the proportion of nursery-grown plants which set bud on the 24th of September in the second growing season.

A strong additive mode of inheritance has been observed for other tree characters as well. In *Pinus silvestris* it was reported for height growth, (Nilsson 1970; Johnsson 1973) for resistance against *Melampsora pinitorqua*,

Table 6. Variance-ratios for testing hypotheses concerning general combining ability (GCA) and specific combining ability (SCA)

Character	GCA between / GCA within	GCA within / Error	GCA within / SCA within	SCA between / SCA within	SCA within / Error
1st growth period					
Critical night length	46.26***	5.74***	5.41**	9.00**	1.06
2nd growth period					
Bud-set	15.35*	14.51***	2.48	0.00	5.86***
Bud-stage 3	19.21*	1.96	0.65	0.60	3.01*
Bud-stage 4.5	13.01*	2.57	3.40	3.05	0.76
Bud-stage 6	6.92	2.07	1.59	0.80	1.30
3rd growth period					
Bud-set	7.24	15.46***	5.26*	0.84	2.94*
Bud-stage 3	20.66*	6.09***	2.48	0.42	2.46*
Bud-stage 4.5	22.31**	7.50***	2.65	0.70	2.83*
Bud-stage 6	50.10***	2.33	1.21	2.91	1.93

Error = error mean square (within blocks and treatments)

Significance at the 5, 1 and 0.1 per cent level is denoted by one, two and three asterisks, respectively

Table 7. Estimated values of variance components. The estimates have been made (1) without respect to the grouping into provenances, and (2) 'within' provenances. (Cf text.)

Character	Estimate of σ_g^2		Estimate of σ_s^2		Ratio between estimates (σ_s^2/σ_g^2)	
	(1)	(2)	(1)	(2)	(1)	(2)
1st growth period						
Critical night length	0.356	0.043	0.027	0.003	0.08	0.06
2nd growth period						
Bud-set	21.4	3.4	5.7	6.9	0.27	2.02
Bud-stage 3	0.74	0	0.63	0.69	0.85	–
Bud-stage 4.5	0.63	0.14	0	0	0	0
Bud-stage 6	0.43	0.09	0.11	0.13	0.26	1.33
3rd growth period						
Bud-set	64.2	25.8	13.0	13.5	0.20	0.52
Bud-stage 3	3.05	0.40	0.47	0.55	0.15	1.36
Bud-stage 4.5	3.37	0.43	0.53	0.57	0.16	1.32
Bud-stage 6	3.15	0.06	0.68	0.43	0.22	7.77

(Martinsson 1975) for susceptibility to *Lophodermium pinastri* (Johnsson 1976a) and for the origin of empty seeds (Johnsson 1976b). In *Picea sitchensis*, Samuel et al. (1972) observed that tree form characters were inherited in a predominantly additive manner, whereas characters of tree vigour were controlled by both additive and non-additive effects.

Breeding Values

The breeding values constitute the additive components in the mathematical model (1). They were estimated by the method of least squares. For the individual clones, the estimated breeding values for the bud-set and bud-flushing characters are given as percentages of the mean values in Figure 33 and Figure 34, respectively.

For both the bud-set and bud-flushing characters, the breeding values of the French clones were larger than for the Swedish clones. For bud-set the same ranking of the clones with respect to their breeding values was observed in the 1st and 2nd growth period. Transpositions occurred in the 3rd growth period both within the French and Swedish group. In the 2nd and 3rd growth periods the bud-flushing characters showed, with three exceptions, the same ranking of the clones as for bud-set in the 1st growth period. This means that clones characterized by an early bud-burst also showed an early bud-formation (short critical night length).

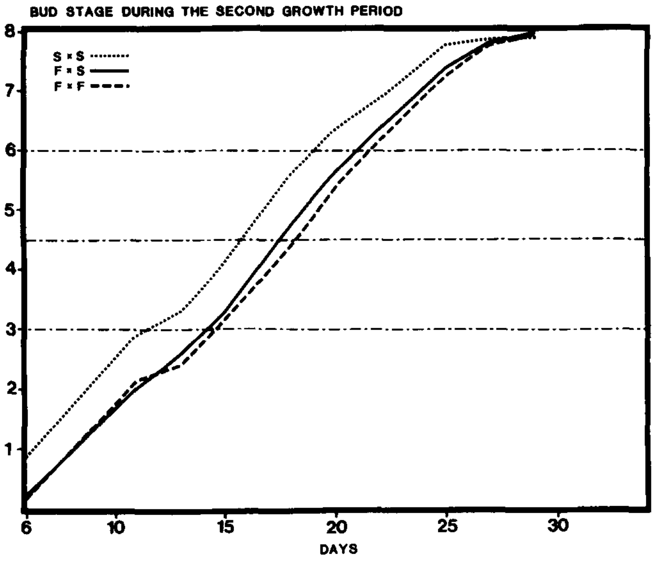


Fig. 31

Figs. 31-32. Average curves for the bud-flushing during the second and third growth period. The curves are based on the mean values for the progenies of the intra- and interprovenance crosses in the diallel of Fig. 9

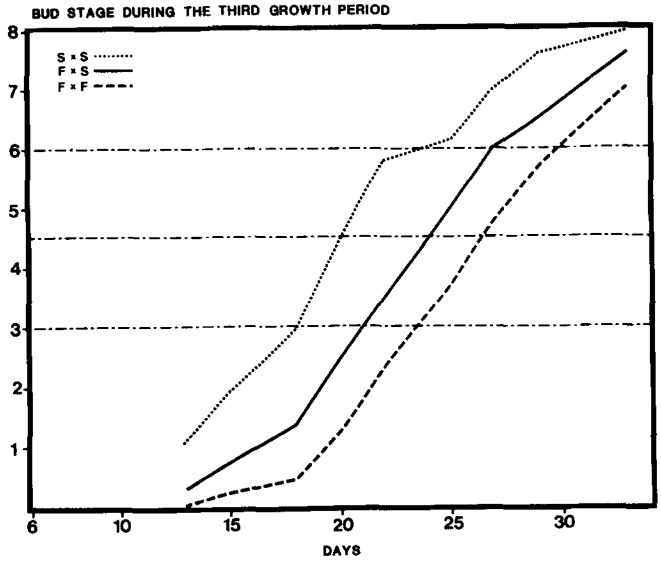


Fig. 32

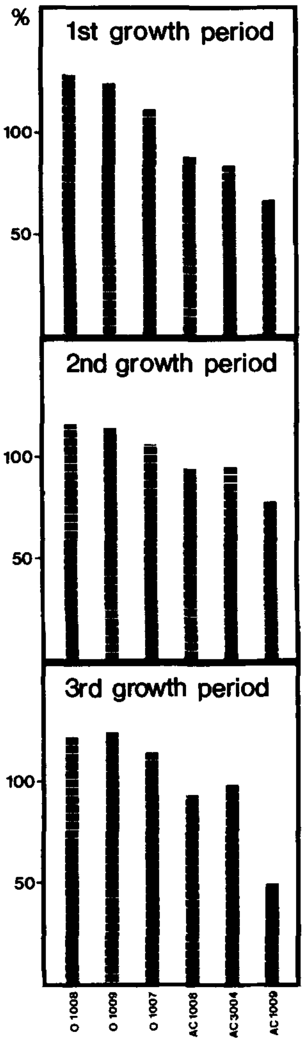


Fig. 33. Estimated breeding values for bud-set of three French clones (O-clones) and three Swedish clones (AC-clones). The 1st growth period refers to critical night length for bud-set; the 2nd and 3rd growth period refer to mean days to bud-set

The deviation of the individual hybrid progenies from additivity are illustrated in Figures 35-36 for the different characters. These deviations constitute the difference between the observed value and the expected value for additive gene action which is obtained by adding the estimated breeding values of the parental clones.

For the bud-set characters, most of the deviations were negative, indicating that the interprovenance hybrids to a great extent behave like their Swedish parents. For example, all hybrid progenies but one deviated towards the short Swedish critical night length. For the character of flushing, however, most of the deviations were towards the late French bud-break.

For breeding purposes it may be concluded that the deviations from an intermediary behaviour of the interprovenance hybrids were favourable for both characters if the hybrids are to be planted in Sweden.

Concluding Remarks

The main purpose of the present investigation was to determine the photoperiodic response for bud-set and the temperature requirements for bud-flushing of the interprovenance hybrids compared to the performance of the parents in intraprovenence crosses. As seen from Figs.

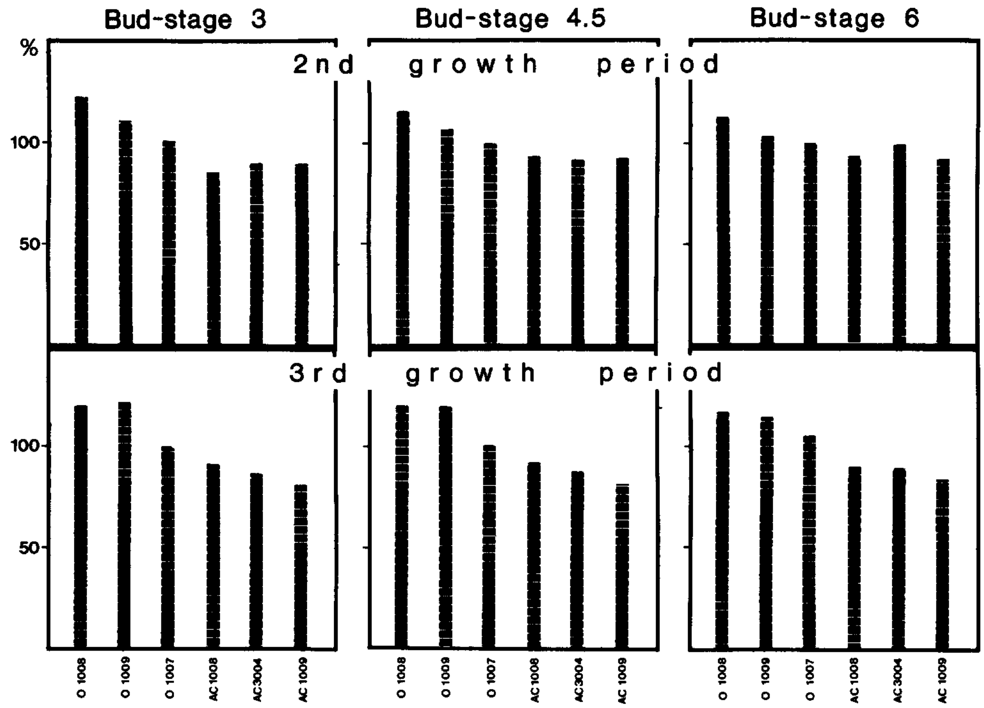


Fig. 34. Estimated breeding values for bud-flushing of three French clones (0-clones) and three Swedish clones (AC-clones) in the 2nd and 3rd growth period

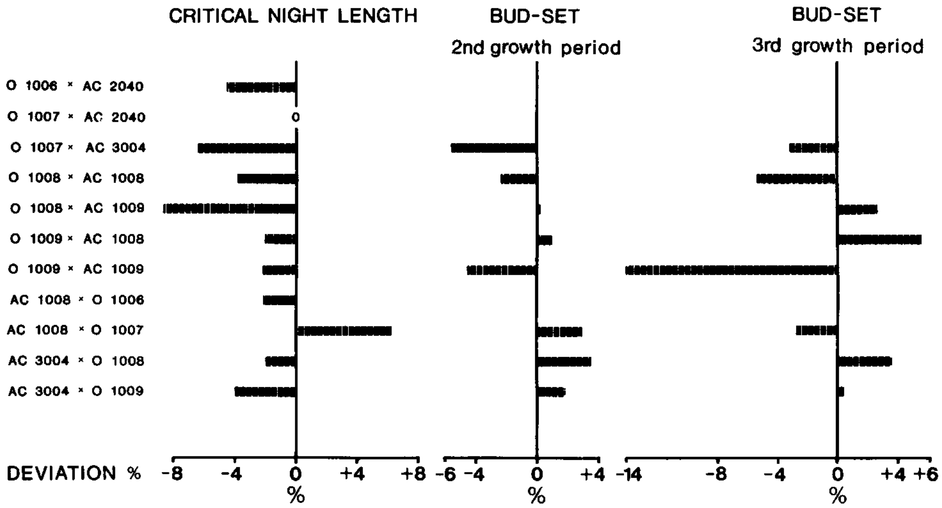


Fig. 35. Deviation in the hybrids from expectation of additive gene action in the characters critical night length for bud-set of growth period 1 and mean days to bud-set in growth period 2 and 3

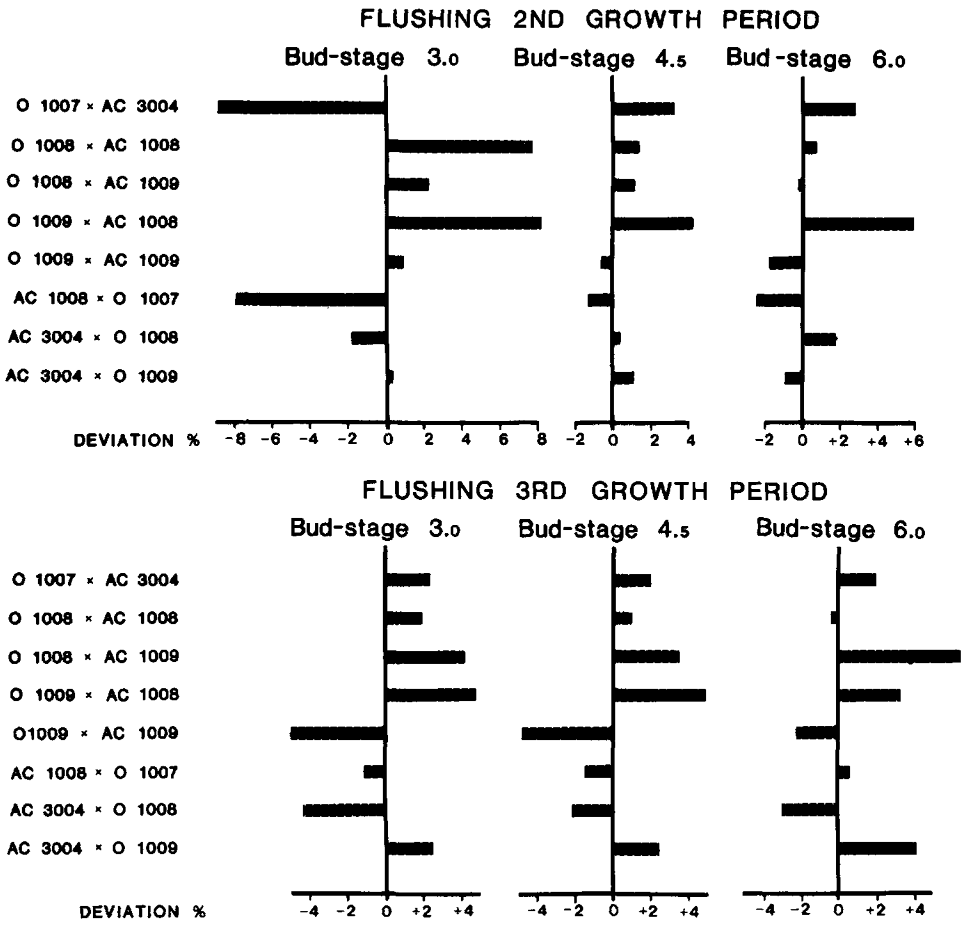


Fig. 36. Deviation in the hybrids from expectation of additive gene action in the character bud-flushing studied in growth period 2 and 3

20-22 and 31-32, which summarize graphically the results obtained, the mean curve of the hybrids occupies an intermediate position for the characters studied. Yet an analysis of individual progenies reveals a wide variation of interprovenance hybrids showing, for example, the short critical night length for bud-set, characteristic of the Swedish clones, or the late bud-flushing date, characteristic of the French parent clones. The prevalence of additive gene action is brought out by the analysis of variance. The observed differences among crosses could be attributed to differences in the general combining ability of individuals of the two provenances. Within provenances, hybrid progenies with specific photoperiodic characteristics appear to be present.

These findings suggest that the photoperiodic and temperature response are determined and influenced by a considerable number of genes and/or alleles with small additive effects. A provenance population harbours different combinations and frequencies of these genes and a successful breeding program based on interprovenance crosses requires the identification of suitable parents. This can be done by the evaluation of hybrid seedlings in the manner presented in this paper. It should be recalled that each provenance was represented by only a few individuals, four trees in the critical night length experiment and three trees for the other characters studied. In addition, these trees were classified as plus trees and need therefore not be representative of the provenance.

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Literature

Dormling, I.: Photoperiodic control of growth and cessation in Norway spruce seedlings. – IUFRO Division 2, Working Party 2.01.4 Growth Processes Symposium on Dormancy in Trees, Kórnik, Sept. 5-9, 16 pp. (1973)

Dormling, I.; Gustafsson, A.; Wettstein, D. von: The experimental control of the life cycle in *Picea abies* (L.) *Karst*. I. Some basic experiments on the vegetative cycle. Silvae Genet. **17**, 44-64 (1968)

Dormling, I.; Ekberg, I.; Eriksson, G.; Wettstein, D. von: The inheritance of the critical night length for budset in *Picea abies* (L.) *Karst*. Proc. Joint IUFRO Meeting, S. 02.04.1-3 Stockholm, Session VI, 439-448 (1974)

Ekberg, I.; Dormling, I.; Eriksson, G.; Wettstein, D. von: Inheritance of the photoperiodic response in forest trees. Tree Physiology and Yield Improvement (eds. Cannell, M.G.A.; Last, F.T.) pp. 207-221. New York: Acad. Press 1976

Eriksson, G.; Kiellander, C.L.; Krutzsch, P.: Skogsförnyelse ur genetisk synvinkel. Sv. Skogsvårdsförb. Tidskr. **72**, 143-156 (1974)

Heide, O.M.: Growth and dormancy in Norway spruce ecotypes II. Aftereffects of photoperiod and temperature on growth and development in subsequent years. Physiol. Plant **31**, 131-139 (1974)

Hinkelmann, K.: Two-level diallel cross experiments. Silvae Genet. **23**, 18-22 (1974)

Holzer, K.: Die Vererbung von physiologischen und morphologischen Eigenschaften bei der Fichte. I. Sämlungsuntersuchungen. Mitt. Forstl. Bundesvers. Anst., Mariabrunn **71**, 1-185 (1966)

Holzer, K.; Nather, J.: Die Identifizierung von forstlichem Vermehrungsgut (The identification of forest reproductive material). In: '100 Jahre Forstliche Bundesversuchsanstalt', Forstl. Bundesvers. Anst. Wien, 13-42 (1974)

Håbjørg, A.: Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of *Betula pubescens* Ehrh. Meldinger Norges Landbrukshógskole **51**, 1-27 (1972)

Johnsson, H.: Avkommeprövning av björk – preliminäre resultat från unga försöksplanteringar. Svensk Papperstidn. **11**, 379-393; **12**, 412-426 (1951)

Johnsson, H.: Avkommeprövning av en tallfröplantage; baserad på tioåriga avkommor. Fören. Skogsträdsförädling, Inst. för skogsförbättring, Årsbok 1972, 140-159 (1973)

Johnsson, H.: Angrepp av tallskytte (*Lophodermium pinastri*) i en 6 × 6 diallel av *Pinus silvestris*. Fören. Skogsträdsförädling, Inst. för skogsförbättring, Årsbok 1975, 74-78 (1976a)

Johnsson, H.: Contributions to the genetics of empty grains in the seed of pine (*Pinus silvestris*). Silvae Genet. **25**, 10-15 (1976b)

Johnsson, H.: Syd- och nordförflyttning av björkprovenienser. Fören. Skogsträdsförädling, Inst. för skogsförbättring, Årsbok 1976, 48-61 (1977)

Krutzsch, P.: Norway spruce. Development of buds. IUFRO S.2.02.11., p. 1-4 (1973)

Langlet, O.: Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus silvestris* L.). Medd. Statens Skogsförsöksanst. **33**, 295-330 (1943)

Magnesen, S.: Eksperimental-økologiske undersøkelser over vekstavslutningen hos frøplanter av gran (*Picea abies* (L.) *Karts.*) 3. Virkning av daglengde supplerende forsøk med 53 frøpartier. Medd. Vestlandets forst. forsøkssta. **52**, 273-317 (1972)

Morgenstern, E.K.: Genetic variation in seedlings of *Picea mariana* (Mill.) BSP. I. Correlation with ecological factors. Silvae Genet. **18**, 151-161. (1969)

Martinsson, O.: Resistensprövning mot parasitsvampar. Sv. Skogsvårdsförb. Tidskr. **73**, 31-46 (1975)

Nilsson, B.: Racial hybridization in *Pinus silvestris*. Analysis of a partial diallel cross design. Department of Forest Genetics, Research Notes **8**, 1-7 (1970)

Pauley, S.; Perry, T.: Ecotypic variation of the photoperiodic response in *Populus*. J. Arnold Arboretum **35**, 167-188 (1954)

Samuel, C.J.A.; Johnstone, R.C.B.; Fletcher, A.M.: A diallel cross in Sitka spruce. Assessment of first year characters in an early glasshouse test. Theoret. Appl. Genet. **42**, 53-61 (1972)

Sylvén, N.: Longday and shortday types of Swedish forest trees. Medd. Fören. Växtförädling Skogsträd (English summary) Sv. Papp. Tidn. **43**, 351-354 (1940)

Tho, T.: Analyse av diallele krysningsavkom i vanlig gran (*Picea abies* (L.) *Karst.*). Norsk institutt for skogforskning. Avdeling for planteforedling. Thesis. 134 pp. (1977)

Vaartaja, O.: Evidence of photoperiodic ecotypes in trees. Ecol. Monographs **29**, 91-111 (1959)

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G. Eriksson
I. Ekberg
Department of Forest Genetics
Swedish University of Agricultural
Sciences, Box 7027
S-750 07 Uppsala (Sweden)

I. Dormling
B. Matérn
Department of Forest Biometry
Swedish University of Agricultural
Sciences
S-104 05 Stockhom (Sweden)

D. von Wettstein
Department of Physiology
Carlsberg Laboratory
Gl. Carlsberg Vej 10
DK-2500 Copenhagen Valby (Denmark)