

be effectively formulated. Finally, those field test sites which are inevitably "lost" because of rare climatic events such as drought, ice storms, frost, and wind storms must be closely scrutinized for the information they provide.

#### Acknowledgements

We thank the cooperators who established and have maintained these tests for 25 years. We also appreciate the nearly 20 years of devoted service of STAN DILL to this project. Finally, the comments of several reviewers substantially improved the presentation of this manuscript: Dr. TOM ADAMS, Dr. BOB CAMPBELL, Dr. DON LESTER, Dr. FRANK SORENSEN, and two anonymous reviewers.

#### Literature Cited

ADAMS, W. T. and R. K. CAMPBELL: Genetic adaptation and seed source specificity. In: Proc. workshop: Reforestation of skeletal soils. (S. D. HOBBS and O. T. HELGERSON Eds.). Medford, Oregon, 78-85 (1981). — BRUCE, D. and D. J. DEMARS: Volume equations for second-growth Douglas-fir. USDA For. Serv. Res. Note PNW-239. 5 pp. (1974). — CAMPBELL R. K.: Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60: 1036-1050 (1979). — CAMPBELL, R. K. and F. C. SORENSEN: Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. Theor. Appl. Genet. 51: 233-246 (1978). — CHING, K. K.: Early growth of Douglas-fir in a reciprocal planting. Res. Pap. 3, For. Res. Lab., Oregon State Univ., Corvallis (1965). — CHING, K. K. and D. BEVER: Provenance study of Douglas-fir in the Pacific Northwest region. I. Nursery performance. Silvae Genet. 9: 11-17 (1960). — CHING, K. K. and P. N. HINZ: Provenance study of Douglas-fir in the Pacific Northwest region. III. Field performance at age twenty years. Silvae Genet. 27: 229-233 (1978). — COCHRAN, W. G. and G. M. COX: Experimental designs. John Wiley and Sons, New York. 611 pp. (1957). — CONKLE, M. T.:

Growth data for 29 years from the California elevational transect study of ponderosa pine. For. Sci. 19: 31-39 (1973). — HEINER, T. C. and D. P. LAVENDER: Early growth and drought avoidance in Douglas-fir seedlings. Res. Pap. 14, For. Res. Lab., Oregon State Univ., Corvallis (1972). — KING, J. E.: Site index curves for Douglas-fir in the Pacific Northwest. Weyerhaeuser For. Pap. 8, Centralia, Washington. 49 pp. (1966). — LAVENDER, D. P. and W. S. OVERTON: Thermoperiods and soil temperatures as they affect growth and dormancy of Douglas-fir seedlings of different geographic origin. Res. Pap. 13, For. Res. Lab., Oregon State Univ., Corvallis (1972). — LAVENDER, D. P., K. K. CHING and R. K. HERMANN: Effect of the environment on the development of dormancy and growth of Douglas-fir seedlings. Bot. Gaz. 129: 70-83 (1968). — NAMKOONG, G.: Nonoptimality of local races. Proc. Tenth South. For. Tree Improv. Conf., 149-153 (1969). — NAMKOONG, G. and M. T. CONKLE: Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22: 2-12 (1976). — NAMKOONG, G., R. A. USANIS and R. R. SILEN: Age-related variation in genetic control of height growth in Douglas-fir. Theor. and Appl. Genet. 42: 151-159 (1972). — ROWE, K. E. and K. K. CHING: Provenance study of Douglas-fir in the Pacific Northwest region. II. Field performance at age nine. Silvae Genet. 22: 93-147 (1973). — SILEN, R. R.: A simple, progressive tree improvement program for Douglas-fir. USDA For. Serv. Res. Note PNW-45. 13 pp. (1966). — SILEN, R. R. and N. L. MANDEL: Clinal genetic growth variation within two Douglas-fir breeding zones. J. For. 81: 216-220, 227 (1983). — SILEN, R. R. and J. G. WHEAT: Progressive tree improvement program in coastal Douglas-fir. J. For. 77: 78-83 (1979). — WESTERN FOREST TREE SEED COUNCIL: Oregon and Washington tree seed zones. USDA For. Serv., Pac. Northwest Reg., Portland, Oregon (1973). — WHITE, T. L., K. K. CHING and J. WALTERS: Effects of provenance, years, and planting location on bud burst of Douglas-fir. For. Sci. 25: 161-167 (1979). — WHITE, T. L., D. P. LAVENDER, K. K. CHING and P. HINZ: First-year height growth of southwestern Douglas-fir in three test environments. Silvae Genet. 30: 173-178 (1981).

## Flowering in Norway Spruce Seed Orchards

By T. SKRØPPA and R. TUTTUREN

Norwegian Forest Research Institute,  
1432 Aas-NLH, Norway

(Received 17th September 1984)

#### Summary

Female and male flowering have been assessed during ten years in six Norway spruce seed orchards, and during three years in a clonal archive. A large variation in flowering is observed between sites, between years within each site, between provenances, and between clones of the same provenance within the orchard. Depending on environmental conditions for flowering, a certain percentage of the clones in each orchard can be expected to have none, or very modest, flowering most years. Flowering is also affected by latitudinal and altitudinal transfers of the clones.

*Key words:* *Picea abies*, flowering, seed orchards.

#### Zusammenfassung

In einer Periode von 10 Jahren wurde auf sechs norwegischen Fichten-Samenplantagen das männliche und weibliche Blühverhalten bonitiert. Das gleiche wurde in einem Klon-Archiv vorgenommen, jedoch nur über einen Zeitraum von drei Jahren. Es wurden zwischen den verschiedenen Standorten, zwischen den Jahren innerhalb der einzelnen Standorte, zwischen den Provenienzen und zwischen den Klonen ein und derselben Provenienz große Unterschiede im Blühen festgestellt. In Abhängigkeit von den Umweltbedingungen zeigt sich, daß in den meisten Jahren ein bestimmter Prozentsatz der Klone auf jeder Plantage nur gering oder gar nicht blüht. Einfluß auf das Blühen hat auch ein

Verbringen der Klone in andere Breitengrade oder andere Höhenlagen.

#### Introduction

Frequent and abundant flowering of a large proportion of the clones is essential for the success of a clonal seed orchard breeding program. With Norway spruce (*Picea abies* (L.) KARST.), flowering in seed orchards has been variable, and seed yields have, with few exceptions, been low compared to other species (SAMUELSON, 1979). The observed variation in flowering parallels to the variability found in natural stands. Norway spruce flowers at irregular intervals with large regional differences. Within the Nordic countries, the amount of seed produced in a stand decreases from south to north, and from low to high altitudes (SARVAS, 1957; HAGNER, 1965). Differentiation of reproductive buds is affected by favourable environmental conditions, and temperature is one significant factor influencing this process (TIREN, 1935; BRØNDBO, 1970; LINDGREN *et al.*, 1977). Other environmental variables, such as light intensity, water conditions, and nutritional status are also important. A recent review of the flower induction process in Norway spruce is provided by DUNBERG (1979).

The present paper reports results from ten years of flowering assessments in six Norwegian seed orchards, compri-

Table 1. — Location and characteristics of the six seedorchards and the clonal archive included in the study.

	Years of grafting	Area size ha	Number of clones	Graft heights in 1980, m	Years of assessments	Origin of clones	Altitude m a.s.l.
Seed orchards:							
Eloy	1969	3	55	3-4	1974-83	Southeastern Norway	40-310
Sauherad	1969	8	79	7-8	1974-83	Southeastern Norway	325-830
Svenneby	1966-67	24	211	6-9	1974-83	Southeastern Norway	325-620
Kaupanger	1967-68	16	172	7	1974-83	Southeastern Norway	700-925
Lyngdal	1969-70	10	195	3.5-5	1974-83	Central Norway	< 500
Romsa	1962-63	10	228	10	1970-79	Norway, Central Europe	
Clonal archive:							
Rodser	1961-63		366		1970, 73, 76	Norway, Central Europe	

sing 940 clones. Flowering has also been studied in a clonal archive. These assessments were initiated as part of a study to assess annual variation in flowering, both among geographically widely scattered locations and among the clones within each seed orchard. Knowledge of among site variation is important for choice of future locations for new seed orchards, while knowledge of clonal variation is necessary if flowering and reproductive traits are considered for use in selection. Previously, ERIKSSON *et al.* (1973) have observed substantial clonal variation within a Norway spruce seed orchard for the amount of flowers. A large variation has also been observed for the age at which the clones first start to flower. However, little quantitative information is available about the genetic variation in flowering traits, and no inheritance parameters have been

presented for Norway spruce as have been found for other species (SCHMIDTLING, 1981, 1983).

### Material and Methods

A routine assessment of the amounts of female and male flowers is performed every spring in several Norwegian seed orchards. The present investigation is based on data from such assessments in six Norway spruce seed orchards and one clonal archive (Fig. 1, Table 1). Two of the orchards are located in West Norway; one close to the coast and one about 100 km from the coast, one orchard is located in the southern-most part of Norway, while the three others, and the clonal archive, are in South-eastern Norway. The orchards produce seed for different regeneration zones, and different transfers in latitude and altitude of the orchard clones are involved.

The seed orchards, and clonal archive were all grafted in the field on well-established rootstocks with scions from reproductively mature trees. The original spacing was  $2.5 \times 5.0$  m. Most of the orchards have been thinned to  $5.0 \times 5.0$  m spacing. The seed orchards were grafted in a non-random design with each clone in one or several rows. In the flowering assessments each clonal row is treated as one unit, and its amounts of female and male strobili are scored separately into one of the following five classes:

- 0 = no strobilus observed
- 1 = a few strobili
- 2 = some strobili
- 3 = many strobili
- 4 = large amounts of strobili

As the clones differ in height, this is to some degree taken into consideration in the scoring, making it easier for a small clone to achieve a high score than a tall one. A score of 1 can mean that very few strobili, 1-3 females and 1-30 males, are observed, while 3 or 4 indicates that the clone could contribute considerably to the pollen or cone production in the orchard. A score of 2 for female flowering is considered sufficient for controlled crosses to be made for progeny testing.

In the seed orchards the assessments started four to eight years after grafting in 1970 and 1974, and have been performed for ten years (Table 1). In the clonal archive the flowering has been assessed for only a few years with relatively good flowering. Some of the seed orchards are subdivided into units grafted in different years, and only results from the oldest units, with a sufficient number of clones, are included.

Flowering indexes are calculated for each clone for female and male flowering separately by summing the number of years with a score of 2 or higher. If less than ten percent of the clones in an orchard attained this score for

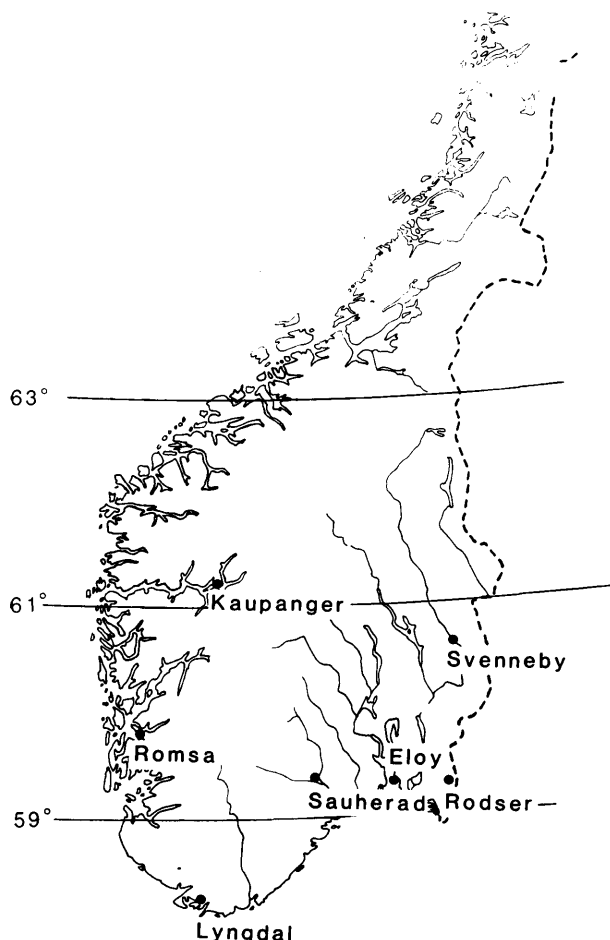


Fig. 1. — Locations of the six seed orchards and the clonal archive.

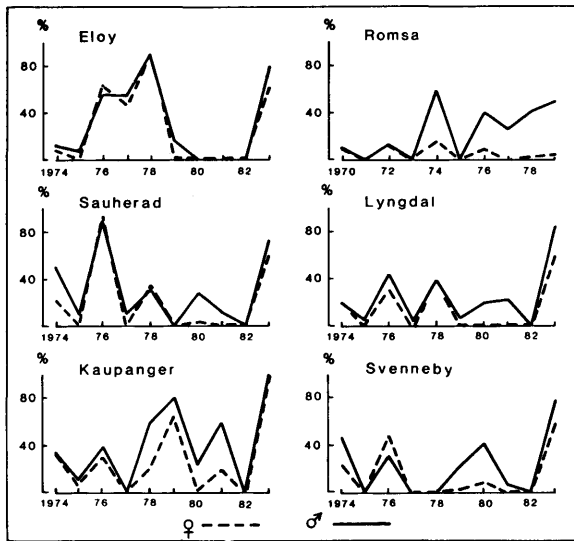


Fig. 2. — Annual variation in flowering for the six seed orchards. Shown are the percentages of clones with a score of 2 or higher.

either female or male flowering, then this year is not included in the index. The reason is that no commercial seed will be collected when flowering is so sparse, neither will any crosses be made. These indexes and their frequency distributions are used for comparing the flowering between different seed orchards and between clones, and also to study the effect of provenance transfers on flowering. The indexes also form the basis for comparison of female and male flowering, and the variation in flowering of the same set of clones at two different sites.

Controlled crosses were performed in three of the seed orchards in 1976 based on a pollen-mix from each orchard. The half-sib families from these crosses were planted at two sites in 1979. Height measurements in 1983, six years after sowing, are used to compare the early growth of a clone's progeny with its flowering ability.

As the flowering assessment data most likely are not normally distributed, non-parametric methods have been used for statistical analyses. Rank correlation coefficients have been calculated between different characters, and non-parametric one-way analyses of variance have been performed.

## Results and Discussion

### Variation in flowering

The general level of flowering differs greatly between the six seed orchards. In addition, a large annual variation is observed within each orchard (Fig. 2). For five of the orchards the years 1976 and 1983 were particularly favourable for flowering, while other years were generally unfavorable. However, interactions between years and locations are present. No flowering was observed in Svenneby in 1978, whilst the flowering was good that year in other orchards. Flowering was abundant in Kaupanger in 1979, but poor on the other sites. As the climate is an important factor influencing flowering (TIREN, 1935; LINDGREN *et al.*, 1977; ILSTEDT & ERIKSSON, 1982) such interactions are most likely caused by differences in local weather conditions during the critical flower induction period. In addition, provenance transfer effects are of importance.

The conditions seem to be particularly unfavourable for female flowering at Romsa, situated on the west coast of Norway (Fig. 2). However, pollen production is satisfactory.

One explanation for these types of differences can be that the low summer temperatures and high humidity on the west coast most often are sufficient for the induction of male strobili, but not for the more demanding female strobili. Climatic conditions appear to be more appropriate in the other seed orchard in West Norway, Kaupanger, located approximately 100 km from the coast.

At Eloy, both female and male flowering were excellent in three consecutive years; 1976, 1977, and 1978. Ten clones were given a score of 3 or 4 for female flowering in each of these three years. This observation is exceptional, as the female strobilus is located to the apex of the twig, and a new strobilus cannot be initiated on the same twig apex until at least one year later. In these cases, female strobili must be located on different branches in any two consecutive years or on different ramets of the same clone. The abundant flowering these three years had a negative effect on the vigour and growth of the grafts in the orchard. However, the low summer temperatures in 1979, 1980, and 1981 resulted in no flowering during the following three successive years, and the vegetative growth resumed. Abundant flowering occurred in 1983, most likely caused by the warm summer the previous year.

Except for Romsa, there is a correlation between good female and male flowering in most years. In some years, however, male flowering is abundant, while female flowering is poor or even lacking, e.g. 1980. This phenomenon has also been observed in Norway spruce stands (SARVAS, 1955, 1957).

Histograms of the frequency distributions of the flowering indexes are shown in Fig. 3 for each of the seed orchards. The general level of flowering seems to have large effect on the shape of the distribution. In the three orchards with the best flowering (Eloy, Sauherad, Kaupanger) only few of the clones have up to 1983 not yet produced female flowers. At Svenneby and up to 1980 at Romsa, however, 30 and 80 percent of the clones have not produced female strobili. The frequency of non-flowering clones is generally

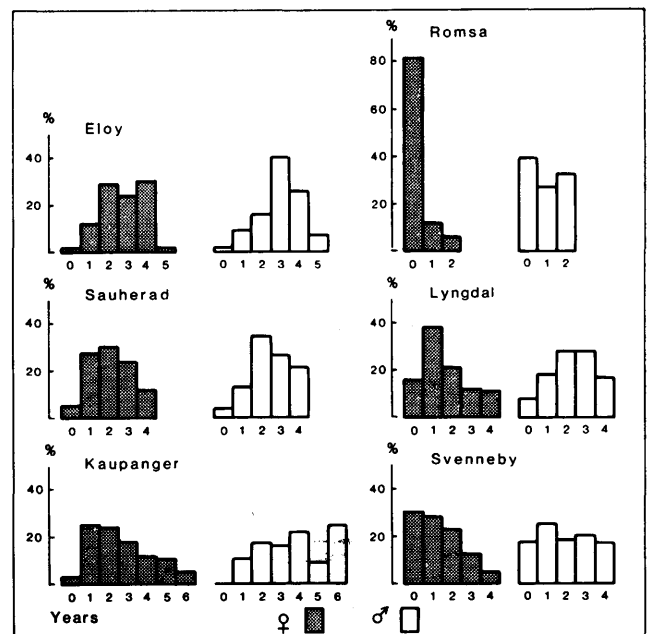


Fig. 3. — Frequency distributions of flowering indexes for the six seed orchards. The index is the number of years with a score of 2 or higher, female and male flowering scored separately.

Table 2. — Mean scores of flowering in 1983 when the clones are grouped according to the index values of flowering in previous years. Clones with an index value of 0 flowered for the first time in 1983.

	Index value of previous years					
	0	1	2	3	4	5
<b>Female flowering:</b>						
Kaupanger	3.05	3.35	3.61	3.67	3.53	3.56
Svenneby	2.68	3.21	3.07	3.91		
Lyngdal	2.84	3.06	3.45	3.70		
<b>Male flowering:</b>						
Kaupanger	3.14	3.19	3.47	3.75	3.82	3.86
Svenneby	2.71	2.87	3.00	3.45		
Lyngdal	2.66	2.85	3.28	3.21		

lower for males than for females, although the differences are small in the three best orchards.

The abundant flowering in 1983 had a large effect on the shape of the distributions. In particular, the number of non-flowering clones was greatly reduced. In Kaupanger, 25.4 percent of the clones had female flowers, and 10.4 percent had male flowers, for the first time in 1983. For Svenneby and Lyngdal the corresponding percentages were 20.9 and 21.3, and 21.0 and 16.4, respectively. Most likely, this is caused both by favourable conditions for flowering in 1983 and by the age of the grafts, resulting in more reproductively mature clones. However, it is not known whether these clones will continue to flower, or whether they will only flower in exceptional years.

Considerable clonal variation exists for precocious flowering, which is here defined as the ability to flower early. This is here measured by the number of years from grafting until the first flowering. Most precocious clones have also flowered regularly in all years favourable for flowering. The assessments in 1983 offers a possibility to look at the relationship between precocity and flowering abundance. Table 2 presents mean scores of clones that flowered in 1983, when the clones are grouped according to the flowering index, based on previous years' performance. Clones with an index value of 0 have flowered for the first time in 1983. This group has the lowest mean score in the three seed orchards\*, both for female and male flowering. Differences among the groups in female and male scoring in 1983 are highly significant in all six cases by non-parametric analysis of variance. The positive correlation between mean flowering score and the flowering index indicates that precocious clones that continued to flower, flowered more abundantly than clones that flowered for the first or second time.

#### A clonal comparison of female and male flowering

The relationship between female and male flowering has been studied using two-way frequency distributions of female and male flowering indexes. These analyses indicate that some clones are good pollen producers, but are below the average for female strobili production. The opposite case, abundant female flowering and poor male flowering, is more unusual. Significant rank correlation coefficients were observed between female and male flowering indexes with estimates varying between  $r = 0.40$  and  $r = 0.66$ . Nevertheless, differences can be found between different years within the same clone; a clone may be an excellent pollen producer with few female strobili one year and the opposite the next flowering event. Rank cor-

\* (Kaupanger, Svenneby and Lyngdal)

relation coefficients between female and male scoring within years vary between  $r = 0.40$  and  $r = 0.70$ .

#### Clones assessed at two sites

Some clones are grafted in two seed orchards and flowering can be compared in two different environments. The rank correlation coefficients between flowering indexes of 23 clones common in Svenneby and Sauherad are estimated to values of  $r = 0.45$  and  $r = 0.48$  for female and male flowering, respectively. The corresponding estimates for 18 clones common in Kaupanger and Romsa are  $r = 0.72$  and  $r = 0.71$ . Non-significant correlations were observed between 13 clones common in Eloy and Romsa. The results indicate a positive relationship between clone's flowering ability at different sites, as long as environmental conditions for flowering are satisfied.

#### Flowering and provenance transfers

The clonal archive at Rodser is comprised of clones originating from different latitudes and altitudes in Norway, and also some clones of Central European origin (Table 1). Histograms of frequency distributions of flowering indexes are shown in Fig. 4 for six groups of clones. For female flowering, the distributions change consistently from low to high frequencies of flowering with increasing elevations in Southern Norway. Close to 40 percent of the clones from the lowest altitudinal zone, which have been transferred least, had no female strobili production during the three years, compared to 25 percent for the two upper zones. For male flowering, there are no clear trends, except that a considerable proportion of clones from the highest altitudes have produced no male strobili. Clones from Central Norway, which are transferred four to seven degrees of latitude southwards, had more female strobili than the clones from the low altitudes in Southern Norway. Thus, a transfer of clones from high to low altitudes, or

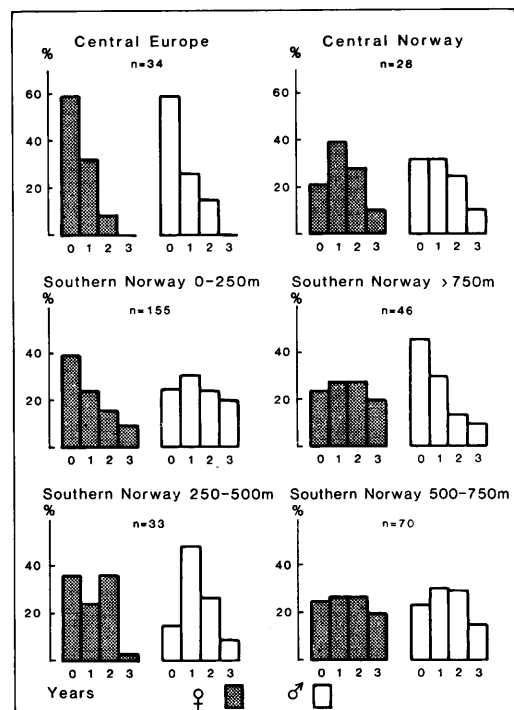


Fig. 4. — Frequency distributions of flowering indexes for different provenance groups at Rodser clonal archive. The index is the number of years with a score of 2 or higher, female and male flowering scored separately.

from northern to southern latitudes, seems to promote female flowering. Transfers from Central Europe to Norway, however, appear to have negative effects on flowering, as 59 percent of those clones had neither female nor male strobili production.

The level of flowering in the six seed orchards is influenced both by the orchard environment and by the type of transfer of the clonal material. With these data it is not possible to separate environmental effects from transfer effects. The clones at Kaupanger, which show the best flowering, benefit both from a favourable climate and from a transfer from high to low altitudes. In Lyngdal, transfers from north to south are of magnitudes from five to nine degrees of latitude. Here, however, climatic conditions are less favourable than in Kaupanger. At Romsa, clones of different origins are grouped into breeding units. The clones that flower most abundantly are either of northerly origin or from high altitudes. Clones of Central European origin flower poorly.

#### *The genetic composition of seed orchard seed*

ERIKSSON *et al.* (1973) studied the occurrences of different mating combinations in a Norway spruce seed orchard and found that four of 20 clones contributed 55 percent of the genes to the seed orchard's offspring. No such figures can be calculated from our studies, but the data show that the genetic composition of the seed will vary considerably between years within the same seed orchard. For example in Kaupanger in 1983, 50 and 60 percent of the clones were rated with the highest score for female and male flowering, respectively. Thus, a potential large number of different matings can be expected. In 1979, on the contrary, the corresponding percentages were 4 and 19. This means that only a few parents were likely to contribute their genes to the offspring of the seed orchard. Similar results can be found for the other seed orchards. The mating pattern will, of course, also depend on the experimental layout and the amount of pollen contamination from outside the orchard. A general rule, however, seems to be that most of the seed collected in a year with limited flowering will originate from a small number of parents, and the parental contribution of genes will be unbalanced. One way to avoid undesired effects of a narrow genetic background is to mix seed from different years.

#### *Early growth of seed orchard progenies*

Significant differences in height growth, four years after planting, were present between controlled-cross half-sib families from three of the seed orchards. The number of families tested were 110, 79, and 55, respectively. These differences were not related to differences in seed weights. Although the maternal parents differ greatly for both female and male strobili production, no significant correlations could be established between flowering characteristics of the parental clones and the height growth of their progenies.

SCHMIDLING (1981) reported negative genetic correlations between flowering and growth traits of loblolly pine, all characters measured in the progeny populations. If such negative correlations were present in Norway spruce, they are not likely to show up until the progenies are sexually mature and have flowered. Our results indicate that it is possible to select progenies with an outstanding early growth also among the heavy cone producers.

#### *Seed production in the orchards*

The first commercial seed crops were harvested in Svenneby and Kaupanger in 1974. In 1976, the seed production was particularly excellent in Sauherad (40 kg/hectar) and Svenneby (20 kg/hectar). Seed for practical use has been harvested in Kaupanger in 1974, 1976, 1978, 1979, and 1983; the total seed yield varying from 21 kg in 1974 to 630 kg in 1983. This last year all seed orchards have produced considerable amounts of seed. Altogether 1826 kg of seed were harvested in the Norwegian seed orchards in 1983. It is, however, difficult to relate the seed yields to the flowering assessments, as the heights of the grafts vary between orchards, and different units of the orchards have been harvested in different years. Cone insects have, in some years, reduced the seed yield of a promising crop.

#### **Conclusions**

The present data can not give any estimates of the relative amounts of genetic versus non-genetic variation of flowering characteristics. Neither can any heritability estimates be calculated. The results demonstrate, however, the presence of a substantial variation in flowering, between different sites, caused by differences in climate and other environmental variables, between years within each site, between provenances, and, finally, between the clones of the same provenance in the orchard. A successful breeding program, based on production of genetically improved seed from seed orchards, should pay attention to this variation. The location of the seed orchard where flowering is optimal is of extreme importance. As long as the relationships between environmental factors and flowering are not fully understood, the best recommendation is to locate the Norway spruce seed orchards to sites with favourable local climates and fertile soils (LSTEDT and ERIKSSON, 1982). Latitudinal and altitudinal transfers of the clones will also affect the flowering. Such transfers may, however, have preconditioning effects in the seed, making the seedlings less fit for their intended planting zone (ROWE, 1964; BJØRNSTAD, 1981).

Clonal variation exists both for the time when the clones start flowering and for the amounts of flowers. This means that the clones can be expected to contribute genes unevenly to the seed harvested in the orchard, particularly the first 15 years after grafting, and in years with less abundant flowering. A certain percentage of the clones can be expected to have little or very modest flowering and can be culled if 1.5 generation orchards are established. This culling requires flowering records for several years. The percentage of non-flowering clones seems to depend on how favourable the conditions are for flowering.

It is possible to influence the flowering in future generation seed orchards by selecting for abundant flowering when individuals are included in the breeding population. However, with the present lack of suitable information concerning the inheritance of flowering traits, and their correlations with growth characters, the gain of this selection is questionable. Rather, it seems much more important to locate the seed orchard to a favourable site.

#### **Literature**

BRØNDBO, P.: The effect of meteorological factors on the flowering intensity and cone crop of *Picea abies* in southeastern Norway. In IUFRO section 22 Working Group on Sexual Reproduction of Forest Trees. Proc. Meeting Varparanta, Finland. 14 pp. (1970). — BJØRNSTAD, A.: Photoperiodical after-effects of parent

plant environment in Norway spruce (*Picea abies* (L.) KARST) seedlings. Meddr Nor. inst. skogforsk 36: 1–30 (1981). — DUNBERG, A.: Flower induction in Norway spruce. In Proceedings of the IUFRO Joint Meeting of Working Parties on Norway Spruce Provenances and Norway Spruce Breeding, Bucharest, p. 137–157 (1979). — ERIKSSON, G., JOHNSON, A. and LINDGREN, D.: Flowering in a clone trial of *Picea abies* KARST. Studia Forestalia Suecica 110: 1–45 (1973). — HAGNER, S.: Cone crop fluctuations in Scots pine and Norway spruce. An investigation based on the cone counts carried out by the National Forest Survey in the years 1954–62 and on the reports submitted by Forest Service rangers on the cone setting in the years 1909–1961. Studia Forestalia Suecica 33: 1–21 (1965). — ILSTEDT, B. and ERIKSSON, G.: Fröproduktion i nordiska fröplantager. 1. Orsaker till spjånader i fröproduktion mellan plantager och år (In Swedish with English summary). Research Notes 33, Swedish University of Agricultural Sciences, Department of Forest Genetics. 1–83 (1982). — LINDGREN, K., EKBERG, I. and ERIKSSON, G.: External factors influencing female flowering in

*Picea abies* (L.) KARST. Studia Forestalia Suecica 142: 1–53 (1977). — ROWE, J. S.: Environmental preconditioning, with special reference to forestry. Ecology 45: 399–403 (1964). — SAMUELSON, K.-R.: Possibilities of seed orchards in Norway spruce. In: Proceedings of the IUFRO Joint Meeting of Working Parties on Norway Spruce Provenances and Norway Spruce Breeding, Bucharest, p. 129–138 (1979). — SARVAS, R.: Investigations into the flowering and seed quality of forest trees. Communicationes Instituti Forestalis Fenniae 45 (7): 1–37 (1955). — SARVAS, R.: Studies on the seed setting of Norway spruce. Meddr norske SkogforsVes. 14: 529–559 (1957). — SCHMIDTLING, R. C.: The inheritance of precocity and its relationship with growth in Loblolly pines. Silvae Genetica 30: 188–192 (1981). — SCHMIDTLING, R. C.: Genetic variation in a loblolly pine (*Pinus taeda* L.) seed orchard. Silvae Genetica 32: 76–79 (1983). — TIREN, L.: Om granens kottsättning, dess periodicitet och samband med temperatur och nederbörd. (In Swedish with English summary). Medd. Statens Skogsförsöksant. 28: 413–454 (1935).

## Heritability Estimates for *Pinus ponderosa* of the Inland Empire

By V. K. GRAHAM<sup>1</sup>), G. M. BLAKE<sup>1</sup>) and H. R. ZUURING<sup>1</sup>)

(Received 18th September 1984)

### Abstract

Genetic variation in seven-year total height of ponderosa pine (*Pinus ponderosa* LAWS.) was estimated. Seven test plantations provided different environmental conditions throughout the Northern Rocky Mountains. Each plantation contains randomized block plantings of 434 open pollinated families representing 93 wild stands selected within the Inland Empire. Two-way analyses of variance with proportional subclasses were performed both within and between plantations. Within each plantation families, blocks and the block x family interaction had significant ( $\alpha = 0.01$ ) effects on the seven-year total height of the progeny. Between selected combinations of plantations significant differences ( $\alpha = 0.01$ ) existed in total height due to family, site and the site x family interaction. Narrow-sense heritability estimates within and between plantations indicated substantial genetic variation. These estimates fall well within the range of other published reports and indicate that this species will respond favorably to selection.

*Key words:* Progeny test, Heritability, Pine, *Pinus ponderosa*, Juvenile tests, Forest genetics.

### Zusammenfassung

Bei *Pinus ponderosa* LAWS. wurde die genetische Variation der Gesamthöhe im Alter 7 geschätzt. Hierzu dienten 7 Versuchsflächen verschiedener Umweltbedingungen in den nördlichen Rocky Mountains. Jede Versuchsfläche enthält randomisierte Blocks mit 434 frei abgeblühten Familien als Nachkommenschaften aus 93 natürlichen Beständen, die im Inland Empire selektiert worden waren. Es wurden Zwei-Wege-Varianzanalysen mit proportionalen Unterklassen innerhalb und zwischen den Flächen durchgeführt. Innerhalb jeder Familie der Versuchsfläche zeigten die Block- und die Block x Familien-Interaktionen Signifikanzeffekte ( $\alpha = 0,01$ ) in der Gesamthöhe der Nachkommenschaft. Zwischen ausgewählten Versuchsflächen-Kombinationen gab es signifikante Differenzen ( $\alpha = 0,01$ ) in der Gesamthöhe, die auf die Familie, den Standort und deren Interaktionen zurückzuführen waren. Heritabilitäts-Schätzwerte im engeren Sinne innerhalb und zwischen Versuchsflächen zeigten eine wesentliche genetische Varia-

tion an. Diese Feststellungen passen zu anderen Veröffentlichungen und zeigen an, daß diese Species auf eine Selektion günstig reagiert.

### Introduction

Previous studies have demonstrated that ponderosa pine is genetically variable for characteristics related to growth (WELLS 1964; SQUILLACE and SILEN 1962, CALLAHAM and LIDDI-COET 1961, WEIDMAN 1939, and others), and early results from provenance research suggests that this variation is adaptive (REHFELDT 1980a).

In this study we examined genetic variation in seven year total height for 434 selected families of ponderosa pine. The specific objectives were: 1) to describe patterns of genetic variation in seven year total height, and 2) to estimate narrow-sense heritabilities in tree height within and between sites.

Genetic variation of ponderosa pine in the northern Rocky Mountains is assumed to relate directly to the complex gradients associated with mountain topography. If so, genetic variation attributable to parent-tree location would best be described by a topocline. The assumption derives from the concept that for any area delimited in space and time, the range of environments can be represented by an average effect and deviations from that average. For plants within such an area, an analogous average genetic effect and deviations exist because adapted plant types occur in proportion to the environment (LEVINS 1969). If there is a gradient change in the environment at several adjacent locations, there should also be a gradual change in genotypes forming a cline (LEVINS 1963). Further, genetic variation among plants within locations along the same gradient can be expected to be proportional to the number of plants sampled within locations (DONOVAN *et al.* 1976).

### Materials and Methods

#### Geographic Area

This study was conceived and implemented by the Inland Empire Tree Improvement Cooperative consisting of members from universities, industries and public agencies

<sup>1</sup>) School of Forestry- University of Montana, Missoula, Montana 59812, USA.