Reproductive Phenology and its Impact on Genetically Improved Seed Production in a Douglas-fir Seed Orchard

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Abstract

Reproductive bud phenology of a Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seed orchard was monitored for two years to determine the validity of one primary seed orchard assumption, namely, that of panmictic equilibrium. The effect of this assumption on seed production was also discussed. The study revealed significant variation in reproductive bud development and overlap between reproductive bud flush of individual trees. These conditions both affect the seed orchard seed quality and quantity by reducing the breeding population size and by lowering seed yield. Two proposals to maximize seed production and genetic efficiency by reducing the effect of panmictic disequilibrium are presented.

Zusammenfassung

In einer Douglasien-Samenplantage *(Pseudotsuga menziesii* (Mirb.) Franco) wurde zwei Jahre lang das Erscheinen der Blütenknospen im Frühjahr untersucht, um die Gültigkeit einer primären Voraussetzung für eine Samenplantage, nämlich ein panmiktisches Gleichgewicht, festzustellen. Der Effekt dieser Voraussetzung auf die Samenproduktion wird ebenfalls diskutiert. In der Untersuchung wurde eine signifikante Variation in der Blütenknospenentwicklung festgestellt und außerdem eine Überlappung im Blühverhalten der einzelnen Bäume. Diese beiden Bedingungen beeinträchtigen die Qualität und Quantität des Samens aus einer Samenplantage, indem diese die Züchtungspopulationsgröße sowie die Samenerntemenge reduzieren. Es werden zwei Vorschläge zur Maximierung der Samenproduktion und der genetischen Effizienz gemacht, indem der Effekt des panmiktischen Ungleichgewichtes verringert wird.

Introduction

The production of genetically improved seed is a major goal of any tree improvement program. The Pacific Forest Products' tree improvement program began in 1964 with selection of the initial parent trees to represent the Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] high elevation breeding population. The first seed orchard was established in 1966 (Fashler and Devitt 1980), two additonal Douglas-fir seed orchards have been established, totalling 11 ha consisting of both first and second generation material.

Future seed orchard management practices will depend upon the effectiveness of current techniques particularly with respect to seed orchard genetic efficiency. Both orchard seed production and seed quality should be maximized to ensure the optimum benefit of genetic improvement. Several conditions are essential to achieve maximum genetic efficiency in wind-pollinated seed orchards. These include: a) isolation from surrounding stands, b) equality of female and male strobili production, c) synchronization between reproductive strobili ripening, d) random mating, e) equal compatibility for all crosses, and f) minimal rates of natural self-fertilization (Eriksson *et al.*, 1973; Fashler and Sziklai, 1980; Woessner and Franklin, 1973).

The purpose of this study was to assess the potential deviation from panmictic equilibrium in a Douglas-fir seed orchard. The reproductive phenology was monitored to dertermine the validity of one basic seed orchard assumption, namely, that of panmictic equilibrium and to discuss its impact on seed production.

Materials and Methods

The Pacific Forest Products Ltd., 3.4 ha high elevation combined clonal-seedling Douglas-fir seed orchard in Victoria, B. C. provided the material for the study. The orchard consists of 63 clones and 39 open-pollinated families representing an elevation range of 450 to 1000 m. For the purpose of pollen and seed management the seed orchard population is differentiated according to elevation zones of 450—599 m, 600—749 m and greater than 750 m. The oldest clonal propagules were established in 1966 and 1968 and the open-pollinated 2 + 0 seedlings were planted in 1971.

The reproductive phenology of each seed orchard tree was monitored every second day throughout the pollination period in 1981 und 1982 according to a phenological classification based on recent work by Ho (1980) and Owens *et al.* (1981). The total number of trees observed by elevation zone is given in *Table 1*. The critical stage of female receptivity was when the seed cone had just emerged fully from the

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Table 1. — Total number of trees observed by elevation zones.

	Clonal Trees						Open-Pollinated Trees					
		1981			1982			1981			1982	
Elevation Zone (m)	No. Clones	Total No. Trees	Av. No. Ramets/ Clone	No. Clones	Total No. Trees	Av. No. Ramets/ Clone	No. Families	Total No. Trees	Av. No. Trees/ Family	No. Families	Total No. Trees	Av. No. Trees/ Family
450 - 599	19	65	3.3	22	109	5.0	21	258	11.7	19	259	13.6
600 - 749	23	87	3.5	28	144	5.1	11	156	13.7	12	176	14.7
750 +	5	19	3.8	9	52	5.7	5	69	13.2	6	86	14.3
TOTAL OR AVERAGE	47	171	3.6	59	305	5.2	37	483	13.1	37	521	14.1

Table 2. — Variation in reproductive bud burst timing within and among elevation zones.

Source of Variation	d.f.	E.M.S.+	Clonal trees						Open-pollinated trees					
			Females			Males			Females			Males		
			1981		1982	1981		1982	1981		1982	1981		1982
			df	MS	df	df	MS	df	df	MS	df	df	MS	df	MS
Among Elev.	e-1	$\sigma^2_2 + K_1\sigma^2_{T/E} + K_3\sigma^2_E$	2	41.59^{ns}	2	2	261.95*	2	2	324.35*	2	2	1065.90*	2	267.56*
					19.43^{ns}			51.96^{ns}			106.49^{ns}				
Trees/ Elev.	e(t-1)	$\sigma^2_2 + K_2\sigma^2_{T/E}$	24	40.40*	29	44	82.35*	56	34	175.78*	34	34	255.92*	34	69.42*
					513.12*			48.15*			51.01*				
Residual	et(r-1)	σ^2_2	29	8.05	21	113	12.41	205	345	18.88	277	421	18.54	437	9.66
					134.62			6.21			9.87				

+ σ^2_c = variance due to differences among ramets (trees) within the same clone (open-pollinated family); $\sigma^2_{T/E}$ = variance due to differences among clones (open-pollinated families; σ^2_E = variance due to the differences among elevation zones; K_1-K_3 are the coefficients of the variance components.

++ The trees/elevation trem was significant ($P < 0.05$) at all cases and was used as the error term for testing the among elevations differences.

* Significant at $P < 0.05$.

ns Not significant at $P < 0.05$.

bud scales [B + 2 (Owens *et al.*, 1981)]. The data of pollen shedding was also recorded. The midpoint dates for optimal female receptivity and pollen shedding was determined for each clone and family and based on this average the pollination period was artificially classified into three equal intervals corresponding to early, intermediate and late reproductive bud development.

Cone samples for early, intermediate and late flowering clones and families were randomly selected to study the relationship between filled seed yield and the phenological observations in each year. Each class was represented by at least three clones and three families with six cones from each of the three clones and families for a total of 54 cones per class. Determination of filled seed counts was made using the soft X-ray technique (Simak and Gustafsson, 1953). The time to female receptivity and to pollen shedding was calculated as the number of days from January 1 and April 1 for 1981 and 1982, respectively. The data were analyzed using the following nested linear model:

$$Y_{ijk} = \mu + E_i + C_{(i)j} + \varepsilon_{(ij)k},$$

where:

Y_{ijh} = number of days of the k^{th} ramet (tree) in the j^{th} clone (family) in the i^{th} elevation,

μ = overall mean,

E_i = effect of the i^{th} elevation zone,

$C_{(i)j}$ = effect of the j^{th} clone (family) within the j^{th} elevation zone,

$\varepsilon_{(i)jk}$ = effect of the k^{th} ramet (tree) within the j^{th} clone (family) within the i^{th} elevation zone = residual error.

Source of variation, degrees of freedom, and expected mean squares for the analysis of variance are given in *Table 2*. Because the number of ramets (trees) within clones (open-pollinated families) differed and the number of clones (open-pollinated families) within elevation zone varied, the experimental design was unbalanced. The method described by Sokal and Rohlf (1969) for calculating the values of the coefficients of variance components (K_1 — K_3) was used. The variance components (σ^2_e, $\sigma^2_{T/E}$, and σ^2_E) were calculated and new mean squares were obtained to be used as denominators of F-ratios.

Results and Discussion

Figure 1 describes the pollination period for families, clones and families and clones combined in 1981 and 1982. The pollination period in 1981 extended from March 29th to April 27th. The maximum number of receptive seed cones occurred at April 13 while the maximum number of shedding pollen cones occurred at April 11. The pollination period in 1982 occurred between April 7th and May 6th and the data of maximum female cone receptivity and for pollen shedding was April 22nd.

There was a ten day shift in the pollination period between 1981 and 1982 with the 1982 trees flowering later. A possible cause for this difference in pollination time is warmer spring temperatures in 1981 versus 1982. *Table 3* gives the total degree-days above 5° C (Holmes and Robertson, 1959) for 1981, 1982 and the long-term average. The cumulative degree-day total for the four months January to April was 266.1 in 1981 or 69.8 % greater than the normal 10 year average. In 1982 the cumulative degree-day total for these same months (136.7) was 12.7 % below normal.

This shift difference in pollination period did not significantly alter the relative position of any specific clone or family for reproductive phenology. The correlation coefficient between bud burst dates for the two years was significant for family females ($r = 0.72$, $p < 0.01$, $n = 39$), family males ($r = 0.86$, $p < 0.05$, $n = 39$), clonal males

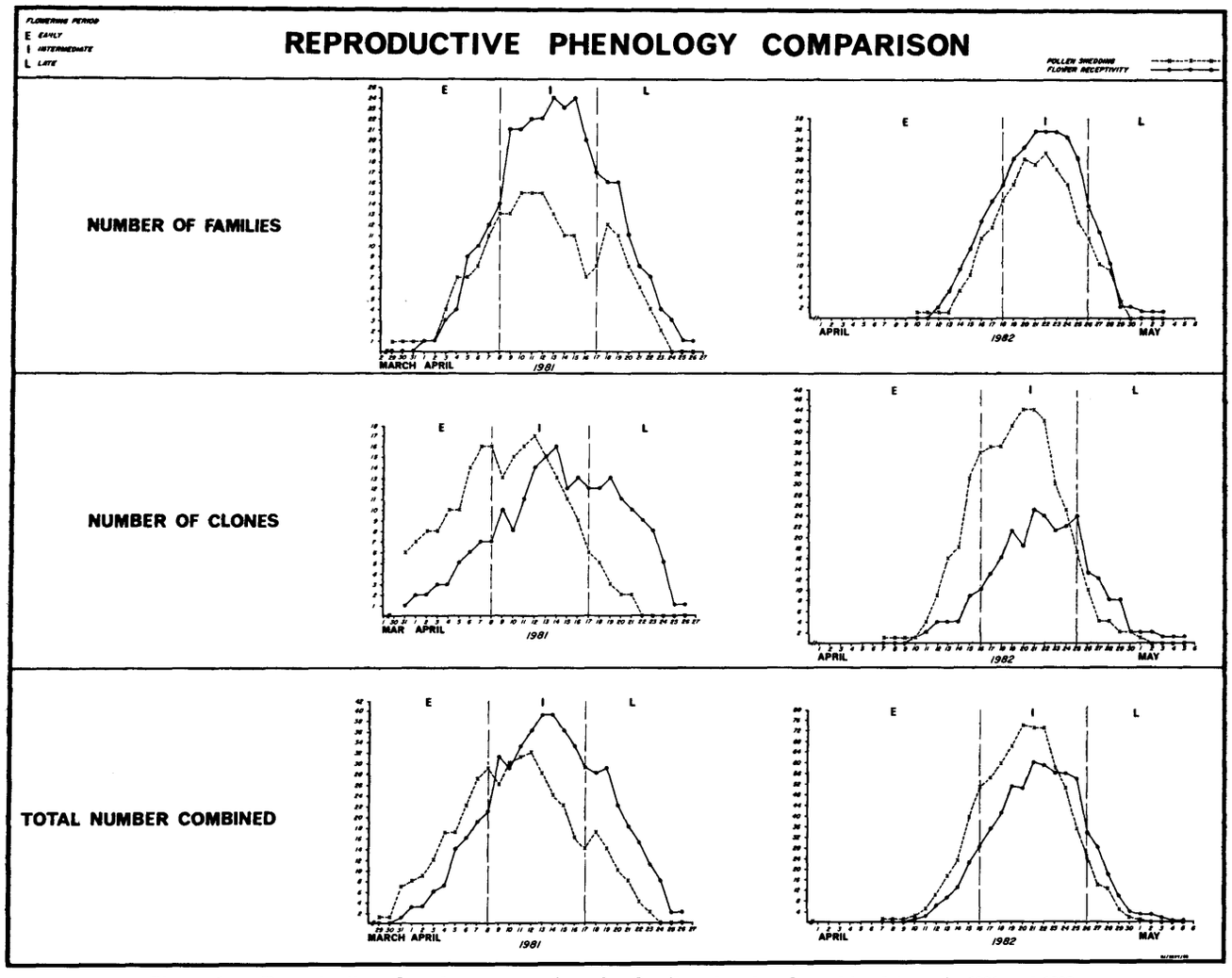

Figure 1. — Reproductive phenology comparison for family, clonal and combined trees in 1981 and 1982.

($r = 0.82$, $p < 0.05$, $n = 46$) and combined family and clonal data ($r = 0.61$, $n = 49$ and $r = 0.78$, $n = 82$, $p < 0.01$). The correlation coefficient was not significant for clonal females ($r = 0.35$, $n = 12$) probably due to the small sample size caused by the absence and/or the presence of certain clones between the two years. The high degree of correlation between relative reproductive bud burst dates in 1981 and 1982 reflects the high degree of genetic control over the bud burst characteristic in forest trees (GRIFFITH, 1968; WORRALL, 1975, 1983).

Table 3. — Degree-Days Above 5° C[1].

Month	1981		1982		Normal	
	Monthly Total	Cum. Total	Monthly Total	Cum. Total	Monthly Total	Cum. Total
January	34.6	34.6	12.7	12.7	14.4	14.4
February	45.6	80.2	31.5	44.2	21.1	35.5
March	82.9	163.1	24.8	69.0	30.6	66.1
April	103.0	266.1	67.7	136.7	90.6	156.7

[1] From: Environment Canada, Atmospheric Environment Service. Monthly Meteorological Summary for the Greater Victoria Region — January, February, March and April, 1981 and 1982. The Victoria airport weather station is approximately 4 Km from the seed orchard.

Large differences among clones and families in dates of seed-cone and pollen-cone bud burst were observed for both years. These differences reached 29 and 25 days between the earliest and the latest clones and families in 1981, respectively *(Fig. 1)*. However, in 1982 the difference was 27 days for both clones and families *(Fig. 1)*. The relatively long period of pollination observed in this study is probably indicative of the whole of Douglas-fir's range since our study material covered a relatively wide region in coastal British Columbia. This long period, typical of Douglas-fir, is characterized by a long spring warm-up (GRIFFITH, 1968; FASHLER and SZIKLAI, 1980).

The long pollination period and its differentiation into early, intermediate and late reproductive bud development classes suggests that major deviation from the panmictic equilibrium within the seed orchard population. The duration of female receptivity ranges from four to six days (OWENS *et al.*, 1981) and the optimal duration of pollen shedding varies between three and five days (BARNER and CHRISTIANSEN, 1962). Therefore clones or families with females receptive in the earliest interval cannot be fertilized by pollen shedding in the latest interval and *vice versa*. These differences in seed orchard reproductive phenology reduce the effective breeding population size and produce a continuum of various breeding population components throughout the pollination period.

Variation within and among the three seed orchard elevation zones is expected from the wide distribution of clones and families. *Table 2* presents the variation in reproductive bud burst timing within and among elevation zones for clones and families in 1981 and 1982. Significant differences were observed for males in dates of pollen shedding while no significant differences were observed for female receptivity. These significant differences for bud burst timing among elevation zones supports the differentiation of the pollination period into different classes (i.e. early, intermediate and late) and the conclusion that panmixis is not occurring.

A disproportionate number of receptive females and shedding pollen buds in each of the three reproductive bud development classes is indicated in *Figure 1*. For the 1981 families, the number of males and females in the early pollination period is approximately equal but the females exceed the males in both the intermediate and the late pollination period. The situation differs slightly for the clones with males exceeding females in the early period, female and male numbers becoming approximately equal in the intermediate period where the bulk of pollination occurs and the females exceeding males in the late period. The combined 1981 information gives an overall excess of males in the early reproductive bud development class and an overall excess of females in the late reproductive bud development class with approximately equivalent numbers of females and males during the middle pollination interval.

The 1982 situation is comparable with males generally exceeding females for early flowering trees and with an abundance of males for the large number of females for intermediate flowering trees. The trees flowering in the later portion of the pollination period appear to have approximately equal numbers of females and males. The difference in available receptive females and available shedding pollen at various stages in the pollination period suggests differences in the viable seed produced in the different reproductive bud development classes.

The seed X-ray analysis was performed with the samples grouped according to clones and families within the early, intermediate and late developmental classes. Whenever possible the same clones and families were used for the 1981 and the 1982 cone collections. Over 12,100 seeds in 1981 and over 11,100 seeds in 1982 were analyzed. *Figure 2* presents the percent filled and percent empty seeds for each phenological class for clonal and open-pollinated trees in 1981 and 1982.

The filled seed percent varied with phenological development class in each year and between years. In 1981 the lowest filled seed percent was produced in the early and in the late pollination phases. 33% and 26%, respectively. The highest filled seed % occurred in the intermediate pollination phase (an average of 50%). Although the overall

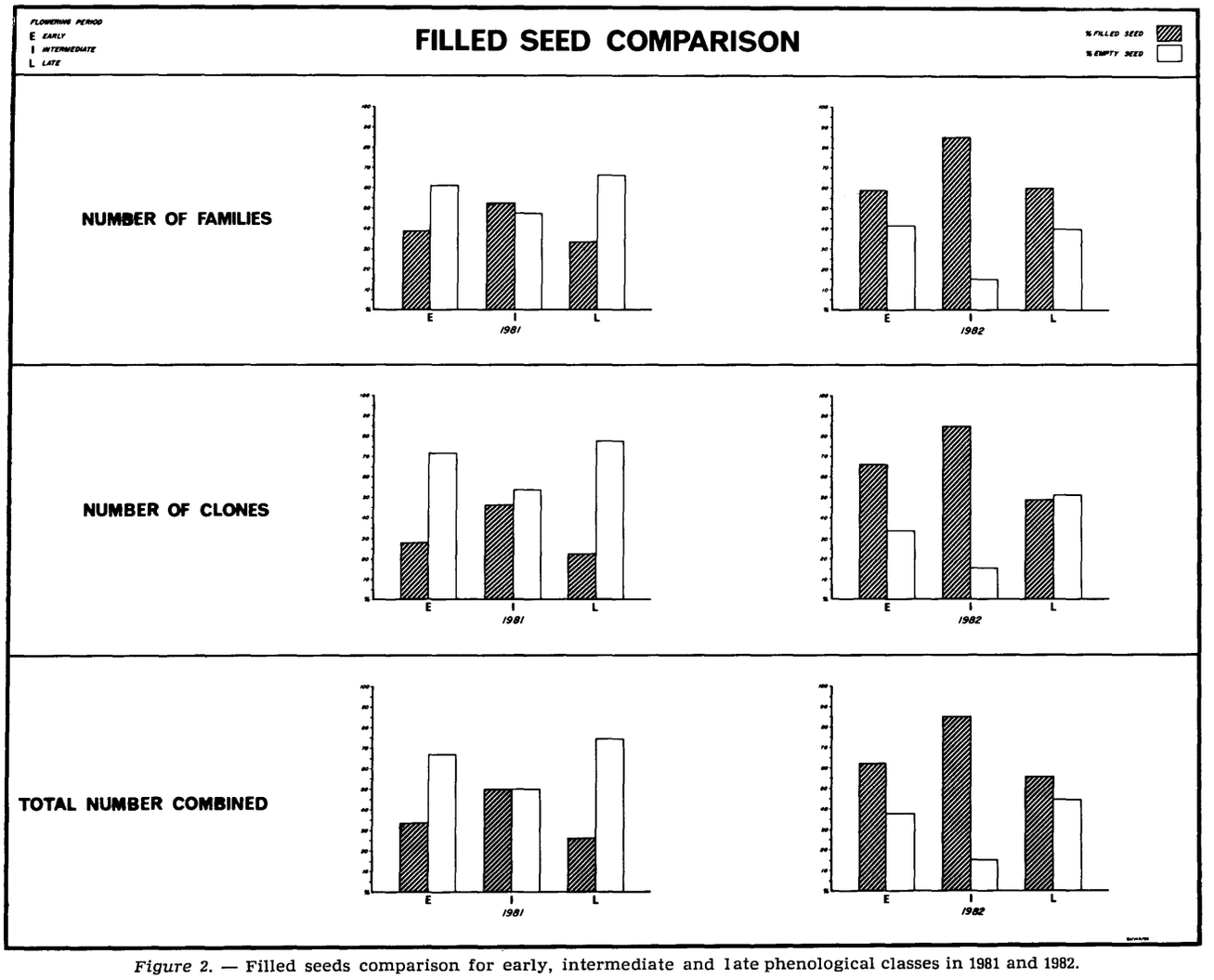

Figure 2. — Filled seeds comparison for early, intermediate and late phenological classes in 1981 and 1982.

filled seed percent was higher in 1982 than in 1981, the 1981 filled seed percent trend was repeated with lower filled seed percent in the early and late phenological development classes, 62.1% and 55.7%, respectively, and higher filled seed percent in the intermediate class (85.0%). The magnitude of percent filled seed differences among the classes also remained very similar in both years with the average difference between the early and late phenological classes in comparison to the intermediate phenological classes 20.4% in 1981 and 26.1% in 1982.

The seed yield results are generally consistent with that predicted from the curves describing reproductive bud development within the seed orchard, namely, that the disproportionate number of receptive females and shedding pollen would result in a difference in filled seeds. The early section of the 1981 and 1982 curves suggested adequate numbers of males compared to numbers of females, however, the seed X-ray analysis indicated lower than expected filled seeds in this section of the pollination period. Possible reasons for this may be that: 1) although pollen is available it may not yet be distributed throughout the seed orchard at appropriate levels to affect complete pollination and 2) the number of different clones and families shedding pollen may not be representative of the amount of available pollen.

This situation is valid only if the source of pollen inside the orchard is coming from the orchard and no outside orchard pollen sources are present. From a pollen contamination study conducted for this seed orchard in 1982 the percent of foreign pollen was estimated from a regression model developed using the frequencies of pollen trapped along transect outside and inside the orchard. The study showed that the pollen release from the surrounding stands coincided with the pollen release inside the orchard but the model indicated no contamination from these stands concided with the pollen release inside the orchard. (Clare, Fashler and El-Kassaby; in preparation).

Bramlett and Popham (1971); Hadders and Koski (1975); O'Reilly *et al.*, (1982); and McKinley and Cunningham (1983) reported in different coniferous species, including Douglas-fir, that a primary cause of empty seeds other than inadequate pollen cloud and depradation factors is embryo abortion caused by homozygous lethal alleles. These recessive lethal alleles are maintained in an open-pollinated mating system. When these embryonic lethal genes reach homozygosity as a product of inbreeding, embryo abortion is expected and lower seed yield is obtained. Estimates of inbreeding in natural Douglas-fir populations indicate levels of about 10% (Sorenson, 1973; El-Kassaby *et al.*, 1981; Shaw and Allard, 1982). Individual tree phenological information indicated overlapping between seed-cone and pollen-cone bud burst in 1981 ($r = 0.63$, $P < 0.01$, $n = 61$) and in 1982 ($r = 0.53$, $P < 0.01$, $n = 67$) and suggests an opportunity for selfing. This potential selfing may be another factor contributing to the lower seed yields obtained in the seed orchard especially in the early and late phenological classes.

Selfing should be minimized or completely eliminated in seed orchards since it causes a loss of vigour negating the effect of genetic improvement (Orr-Ewing, 1954, 1957 and 1965). In addition a high degree of selfing in seed orchard seed will become a factor in parameter estimation from seed orchard test plantations by overestimating the additive genetic variance (Namkoong, 1966).

Conclusion

The study revealed potential problems within the seed orchard population. It appears that reproductive phenology should be an added criterion to be included in the layout and design of future seed orchards to enhance panmixis. Two options are proposed to reduce the effect of panmictic disequilibrium and to maximize seed orchard seed production and genetic efficiency.

The first proposal is the utilization of the irrigation mist system to delay bud development within the seed orchard (Fashler and Devitt, 1980). The cooling treatment can improve panmixis through reduction of the pollination period and thereby increasing the effective breeding population size and increasing the number of crosses available from the seed orchard clones and families.

The second proposal is the intensive application of booster pollination. The effectiveness of this treatment is dependent upon reproductive phenology information to determine the relative reproductive bud burst time for all seed orchard clones and families and preparation of specific pollen mixes at each part of the pollination period to maximize the number of seed orchard crosses. This treatment could later be further refined to favour clonal and or family combinations with high general combining ability.

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Effects of thinning in progeny tests on estimates of genetic parameters in Pinus radiata

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Summary

Data from two progeny tests of *Pinus radiata* were used to examine the effect of thinning on estimates of genetic variances and heritabilities. Each unthinned data set was modified by omitting trees which were subsequently thinned. Heritability estimates for unthinned data were much smaller than for the thinned data. Computer simulated row thinning and selective thinning regimes were also imposed on the otherwise unthinned data sets. Row thinning had no effect but selective thinning produced much higher heritabilities than the unthinned data. The implications of these results and their effects on the way progeny tests are measured are discussed.

Key words: *Pinus radiata*, progeny tests, thinning regimes, heritability estimates.

Zusammenfassung

Daten von zwei Nachkommenschaftsprüfungen wurden dazu benutzt, die Auswirkung der Durchforstung zu Schätzungen der genetischen Varianzen und Heritabilitäten zu untersuchen. Die Daten jedes nicht durchforsteten Bestandes wurden durch das Weglassen der Bäume, die später geschlagen werden sollten, modifiziert. Heritabilitätsschätzungen für die Daten von nicht durchforsteten Beständen waren bedeutend niedriger als für durchforstete.

Eine vom Computer simulierte Reihendurchforstung, sowie selektive Durchforstungsverfahren wurden ebenso an Daten von sonst nicht durchforsteten Beständen vorgenommen. Die Reihendurchforstung zeigte keinen Effekt; die selektive Durchforstung erzeugte dagegen eine weitaus höhere Heritabilität als die Daten der nicht durchforsteten Bestände. Die Folgerung aus diesen Ergebnissen und deren Auswirkungen auf die Art und Weise, wie Nachkommenschaftsprüfungen gemessen werden sollten, stehen noch zur Diskussion.

Introduction

Within a tree breeding program, population genetic parameters such as genetic and environmental variances and covariances are frequently estimated from data collected in progeny tests. Such estimates can be used to calculate the heritability which, in the narrow sense, is the ratio of the addative genetic variance to the total phenotypic variance (FALCONER 1981). This estimates the relative importance of the portion of the genetic variance which is available to recurrent selection programs to predict genetic change following selection. It is widely known that genetic variability is a property which is different for different characteristics in different populations and at different times (FRANKLIN 1979).

The term "progeny testing" strictly applies to the case where the characteristics of progeny are used to assess the breeding value of their parents rather than to make inferences about the progeny themselves (TURNER and YOUNG 1969). Genetic parameters estimated from progeny tests thus apply to the parental population rather than the progeny population. Progeny tests can supply information about the breeding value rankings of parents as individuals as well as about genetic parameters of the parental population.

In forestry, progeny tests usually form a part of some larger forest and are usually thinned at some stage to maintain productivity and/or quality. What effect does this have on the genetic parameters to be estimated? It could be argued that the within-family variance would be reduced by the selective removal of smaller trees and that this would lead to the inflation of heritability estimates where this component of variance forms a large part of the denominator of the heritability ratio (see above). Plots in many progeny tests are small and there may be no justification in using selection theory based on the assumption of a normal distribution. If family differences are based on different distributions of tree size, then selective removal of smaller trees would remove family differences, and the heritability estimate would be reduced. There is also the problem of sampling trees to be measured within a plot. Sometimes the trees are so tall that to measure all trees in a plot would be prohibitively expensive. On what basis should the trees in a plot be selected for measurement in such cases?

Considering that these questions of the effects of thinning and of sampling within families are unresolved and that they affect the very basis of genetic parameter estimation, we were surprised to be unable to find any reference to them in forest genetics literature except for a few papers such as WILUSZ and GIERTYCH (1974) and JAMES (1979) who did not address the problem directly but were concerned with the effects of thinning on the genetic quality of seed collected subsequently. MAUGE *et al.* (1974) stated that total height was "still but slightly heritable" following thinning in a seedling seed orchard implying that the heritability should have been higher. It is not clear whether this implication refers to the thinning or to the time in-