

5.3 Relationship between needle width and resin canal incidence, and frequency distribution of resin canal incidence

Differences between mean widths of needles with 0, 1, 2, and 3 or more resin canals were small, less than the standard deviation of needle width in each class. Mean needle width of a family was not correlated with its mean resin canal frequency. This confirms CRITCHFIELD's observation that the relationship between resin canal frequency and needle width does not appear to be an obligate one in lodgepole pine, and indicates that genetic control of resin canal number is independent of that of needle width.

The frequency distribution of resin canal incidence in seedlings had a large mode at 2.0 resin canals/needle (Fig. 1). As was noted, resin canal number is a countable character. In over 1,100 sections there was no evidence of partial resin canal development (e.g. Figure 3). CRITCHFIELD (1957) noted that one reason for departure from normality in frequency distributions for resin canal incidence is the tendency toward symmetry in the occurrence of resin canals. A needle is most likely to have either 2 or 0 resin canals. This tendency was evident in this study. Of the needles from seedlings which were examined, 622 had 2 resin canals, 218 had 0, only 156 had 1, and 6 had 3. Of needles from grafts, 64 had 2 resin canals and 49 had 0, while only 28 had 1, 5 had 3, and 1 had 5 resin canals. This tendency to symmetry in resin canal occurrence likely contributed to the broad confidence limits for heritability estimates. The frequency distribution of resin canal incidence explains much of the change in terpene distributions in the seedlings caused by scale transformation from absolute to % data (WHITE and NILSSON 1983, Figures 1 and 2). Resin canal distribution is a consideration in genetic studies dealing with characters such as "high" and "low" terpene levels. Resin canal distribution within a tree should be considered when sampling for terpene analysis.

5.4 Concluding remarks

Highly significant correlations between resin canal frequency and absolute amounts of most terpenes indicate that terpene production or storage is compartmentalized in resin canals, and their frequency largely determines the total amount of terpenes in lodgepole pine needles. Heritability estimates based on degree of resemblance of grafts of the same clone, open-pollinated seedlings of the same family, and correlations between open-pollinated progeny and mother trees, indicated that resin canal frequency is

under moderate genetic control. Mother tree position effects on resin canal frequency of scions may give rise to differences in resin canal frequency in grafts taken from the same tree, resulting in variation in terpene production.

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A plan for breeding radiata pine

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Summary

A plan is proposed for improving radiata pine (*Pinus radiata* D. DON) in South Australia. Features of the plan which may be new are: (1) Low cost gene conservation areas which contain the pooled progeny of all parents in

the first-generation breeding population. (2) A two-stage selection scheme, where four individuals are selected from each family in the breeding population (*stage-1*) and then progeny tested using open-pollinated seed (*stage-2*), before finally deciding which two individuals from each family are best for future breeding. (3) An index which employs estimates of GCA to pair potential parents so that more superior families may be generated from single-pair matings.

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Key words: gene pool, two-stage selection, progeny testing, selection index, mating index, seed orchard.

Zusammenfassung

Es wird ein Plan zur Verbesserung der Kiefernart *Pinus radiata* D. DON in Südaustralien vorgeschlagen. Die besonderen, sicherlich neuartigen, Merkmale dieses Planes sind: (1) Niedrige Kosten der Generhaltungsflächen, welche die zusammengefaßte Nachkommenschaft von allen Eltern in der ersten Züchtungsgeneration enthalten. (2) Ein Ausleseverfahren in zwei Stufen, wobei vier einzelne Pflanzen von jeder Nachwuchsfamilie ausgewählt werden (*Stufe-1*) und geprüfte Nachkommenschaften bei Verwendung windbestäubter Samen (*Stufe-2*), bevor man die letzte Entscheidung trifft, wobei zwei Nachkommen von jeder Pflanzenfamilie am besten für die Aufzucht künftiger Generationen geeignet sind. (3) Eine Übersicht bzw. eine Verzeichnis, welches eine Abschätzung des Nachwuchswertes bezüglich der Kreuzung bestimmter Elternpaare ermöglicht, damit die bestmöglichen Eigenschaften aus der Bestäubung desselben Elternpaares erhalten werden können.

Introduction

This article outlines a plan to continue the improvement of radiata pine (*Pinus radiata* D. DON) in the south-east of South Australia. Genetic improvement of radiata pine in the region began in the 1950's, but the current plan has only been in operation since 1980. The objectives of this breeding plan can be summarised as: (1) to continue cumulative improvements already made in the genetic quality of seed used to establish plantations, and (2) maintain the ability of radiata pine to adapt to changing economic and environmental circumstances (i.e. maintain genetic diversity).

Hierarchy of Populations

The main conflict in tree breeding is probably between achieving rapid gains in the genetic quality of seed from orchards, while at the same time attempting to maintain genetic diversity. The solution adopted in this breeding plan is to gradually improve one large breeding population over repeated generations, while concurrently developing from this population a more highly selected seed orchard population of individuals considered 'best' by industry at that time. This strategy creates a hierarchy of populations with three levels: (1) gene pool, (2) breeding population, and (3) seed orchard population. The populations are run in parallel, with all transfer of material from the base to the top of the hierarchy (BURDON *et al.* 1977).

Gene Pool Population

The bottom level of the hierarchy, which is subject to minimal selection, is the gene pool. It is intended to establish the gene pool as bulked plantings of open-pollinated progenies of all plus trees which were in the breeding population at the beginning. The plantings would be at more than one site, for security, and isolated as far as possible from contaminating pollen. The gene pool would be continued after each 'crop' rotation by collecting and replanting open-pollinated seed from a random sample of trees (i.e. zero selection pressure) in each area. Thinning in the gene pool areas could permit the removal of malformed trees but otherwise should be at random.

Under this breeding plan the gene pool serves simply as a low cost 'museum' to conserve traits (or genes) which are present in the breeding population at the beginning but may be lost or discarded in advanced generations. For instance, a museum to conserve attributes such as uninodality over a period of selection favouring multinodal trees.

Genes may be lost from the gene pool in the process of sampling trees for seed to replant the gene pool areas, but provided enough trees are sampled (say 10%), the risk should be acceptable. ROBERTSON (1960) argues that after a population has been through a restriction or 'bottleneck' in population size, such as the initial selection of plus trees for this present gene pool, the genes retained would have their mean frequency in the population increased and therefore become more tolerant to further restrictions. For instance, a gene might be present in one in 10,000 individuals in the unselected population, but if it got through to a gene pool of the progenies of say 700 plus trees, it should be present in at least one in 700 individuals. ("The more highly selected a breed the smaller the numbers needed for storing it"; ROBERTSON 1960).

This type of gene pool is at a disadvantage when individuals are moved from the gene pool to the breeding or perhaps seed orchard populations, because the closeness of their relationship with existing members of those populations is unknown. The advantage of the gene pool is its low cost compared with alternatives such as long-term clone banks. This breeding plan does require clone banks for controlled-pollinations but they are relatively small and short-term. In practice, the present gene pool is supported by extensive plantings in South Australia, and elsewhere, of native provenances of radiata pine (ELDRIDGE 1978), as well as plantings of some selected families from other breeding centres (initiated by C. J. A. SHELBORNE).

Breeding Population

The middle level of the hierarchy is the breeding population and the success of the breeding plan depends largely on cumulative improvement of this population. Most tree breeding programs rely on recurrent selection where superior individuals are selected from the breeding population and crossed in a particular mating pattern to regenerate a new and hopefully improved breeding population for the next generation, and so on.

It is possible to improve the breeding population as (1) a single large population, or smaller, divided breeding groups defined (BURDON and NAMKOONG 1983) as either (2) sublines or (3) multiple populations. There is theoretical evidence to suggest that sublining can provide slightly greater genetic gain in the breeding population after say five to 10 generations (BAKER and CURNOW 1969), although ultimate gains from sublining in the very long-term should be comparable to those from selection in a single undivided population (ROBERTSON 1960; BAKER and CURNOW 1969). However, the main benefit of sublining is perhaps its potential to allow outcrossing among unrelated individuals (taken from different sublines) in advanced-generation seed orchards. This should overcome the inbreeding which would have developed in the advanced-generation breeding population and may, therefore, significantly increase genetic gain in the plantation. A practical problem with sublining could be that the clones in orchards, although unrelated, would be fairly highly inbred and seed production may be reduced. Examples of sublining in tree breeding are provided by MCKEAND and BEINEKE (1980) and WELLENDORF (1982).

Multiple populations differ from sublines in that each population (or line) is selected for different requirements, such as specific adaptation to particular site or silvicultural conditions (NAMKOONG *et al.* 1980; SKRØPPA 1982), or for different combinations of traits in an attempt to guard against improvement in the wrong direction (NAMKOONG

1976; NAMKOONG *et al.* 1980). Indeed, where there are negative genetic correlations between various sets of requirements, multiple populations may be the only worthwhile alternative (SMITH 1969). An instance of multiple population breeding of radiata pine is the proposal to select high growth and high wood density populations in eastern Australia (DEAN *et al.* 1983), and selection of uninodal and multinodal populations in New Zealand (SHELBOURNE, personal comm.).

For the particular circumstances of this breeding plan it was decided to select in a single large population, attempting to develop one line which is generally adapted for a limited set of traits. This decision was taken mainly because of doubts about the managerial resources of the local breeding group to organise and maintain separate lines over a long period. Multiple populations, as distinct from sublimes, seemed quite unnecessary because the region has no particular environments which justify specifically adapted lines, and there are no obvious contradictions in selection criteria which seem to necessitate selecting different populations in different directions.

Selection in the single breeding population will only be for those traits which are most likely to remain economically important in the long-term, such as rapid growth, straight stems, and fine branching (FEDERICK and GRIFFIN 1977). The local industry appears to be less concerned about characteristics such as nodality, and is content to forego selection pressure on this trait in order to achieve greater gains elsewhere. There should be an indirect response towards multinodal stems as a consequence of selection on growth, straightness and branch quality (COTTERILL and ZED 1980). Wood density is an economically important trait but only needs to be maintained at its present level in the breeding population. The mechanics of achieving this will, as described later, depend on index selection with a restriction to hold density constant. There are currently no severe pests or diseases in radiata pine in South Australia; nevertheless it would be foolish not to routinely screen new selections for resistance to well known diseases of the species.

The first-generation breeding population comprises about 200 plus trees selected in the 1950's and 1960's from unimproved plantations throughout Australia and New Zealand, and a further 500 plus trees selected from local unimproved plantations in 1980. This latter addition of plus trees was to make the breeding population as large as practicable from the beginning, and thereby attempt to achieve a reduced rate of inbreeding in subsequent generations (WRIGHT 1931) and maximise genetic progress (ROBERTSON 1960).

Seed Orchard Population

The upper level of the hierarchy is the highly selected seed orchard population, which is a subset of the breeding population. As already mentioned, this strategy of hierarchical populations provides the opportunity to use just a few very superior clones in the seed orchards and thereby achieve substantial short-term gains in the plantation; while genetic diversity is maintained over the long-term in a cumulatively improving breeding population, and a large gene pool (FRANKLIN 1972; LIBBY 1973; BURDON *et al.* 1977).

A major problem is how small and select should the orchard population become? Orchards having just a few highly selected clones will increase the potential productivity of plantations but may undermine plantation stability. It is argued that a narrow genetic base would increase

the risk of plantation failure due to extremes of environment (such as drought in South Australia) or invasion by diseases or insects (HEYBROEK 1978; KLEINSCHMIT 1979; LIBBY 1980). On the other hand there is no guarantee that a wide genetic base (i.e. large orchard population) will render seedling plantations safe from colonisation and subsequent spread of pests (HEYBROEK 1978; LIBBY 1980).

It has been decided to have at least 20 clones in the orchard population of each generation (discussed later). This is approximately the number of clones which have been used in previous orchards in the local breeding region, and the plantations from these orchards have proven stable to years of extreme climate. LIBBY (1980) has made theoretical calculations of the number of clones required for stable clonal plantations and, in so far as his results can be extrapolated to seedling plantations, 20 genotypes in the orchard would appear to give an acceptably low risk of plantation failure.

Selection in the Breeding Population

Classical theory, and results of many experiments with different organisms, indicate that selection in a closed population will lead to a roughly logarithmic ($y = \log x$) decrease in response over generations until a plateau and ultimate limit of selection is eventually reached. This plateauing is due to a cumulative increase in homozygosity caused by genes being either fixed or lost in the process of selection (or random drift), and the associated effect of an increase in inbreeding. The breeder can do little to change the logarithmic nature of the response curve but it is possible to influence the slope of the curve. That is, the short-term and long-term response to selection.

Short-term and Long-term Responses

An advanced-generation breeding plan must be a compromise between achieving rapid gains in the short-term and providing for the highest possible limit of response in the long-term. The main factors which affect this compromise are the intensity of selection and the method of selection, and their interactions with population size (ROBERTSON 1960).

Very intense selection can be expected to give large genetic gain in early generations but at the expense of a lower limit to response in the long-term (ROBERTSON 1960). However, where the population size is reasonably large (such as the 700 parents in the initial breeding population in South Australia) it should be possible to satisfy both short-term and long-term objectives (BAKER and CURNOW 1969; RAWLINGS 1969). SMITH (1969) has calculated that retaining about one in every 100 individuals in each generation should provide good early gains without sacrificing much in the way of ultimate gain after say 20 generations. Calculations of JAMES (1972) lead to a similar conclusion, even for circumstances where the economic value of responses in advanced generations is discounted at up to 10% to give a 'present value' of long-term gains. It will be seen that a selection intensity of about one in 100 individuals has been adopted in the present breeding plan but with the restriction that, after the first generation, selection in the breeding population is applied within-families.

Short-term and long-term gains are also influenced by the method of selection (ROBERTSON 1960; RAWLINGS 1969). FALCONER (1960) gives a non-exhaustive list of alternative methods of selection, of which tree breeders commonly use either family or within-family selection. Family selection can provide very large short-term gains in the breeding

population but in so doing will seriously reduce the effective population size, increase homozygosity and inbreeding, and thereby sacrifice long-term responses (ROBERTSON 1960). Within-family selection should provide good genetic gains in traits with heritabilities above about 0.1 (FALCONER 1960; COTTERILL and ZED 1980), and has the advantage of not greatly reducing the effective population size or substantially increasing the rate of inbreeding. However, selection of phenotypically superior individuals from within-families would not normally provide worthwhile gains in traits with heritabilities below 0.1 (e.g. growth and malformation characteristics of radiata pine in South Australia; COTTERILL and ZED 1980).

In the first-generation of the present breeding plan there is a low intensity selection among families, followed by selection within-families. The 700 parents which constitute the first-generation breeding population occur as female parents in existing open-pollinated (on ortet) progeny tests. The plan is to use the results of these tests, which will be available in the near future, to select the best 400 parents. This initial family selection is intended mainly as a preliminary screening to rid the breeding population, as far as possible, of families (parents) which have an unacceptable incidence of malformations (e.g. forked stems, spiral grain, butt sweep). The intensity of the family selection (retaining 400 in 700) should not be sufficient to seriously reduce long-term gains. One phenotypically superior individual will be chosen from within each of the 400 open-pollinated families retained, and these second-generation selections will be mated in single-pairs to generate a second-generation breeding population of 200 unrelated full-sib families. It is recognised that family and within-family information can be integrated in a combined index approach (ARBEZ *et al.* 1974 *cf.* BURDON 1982), but because of the low inheritance of malformation characteristics it is doubtful whether the combined index would be much more efficient than the independent family and then within-family selection used here (FALCONER 1960).

Selection in the second, and subsequent, breeding populations is entirely within-families but does not rely solely on selection based on individual performance. Instead, there are two stages of selection in each generation, with a 'conventional' *stage-1* selection for phenotypically superior individuals within-families, followed by an open-pollinated progeny test at *stage-2* in which the individuals chosen at *stage-1* are examined more closely (COTTERILL and JAMES 1981). Progeny test selection within-families does not appear to have been used previously in tree breeding and, therefore, the scheme is described in the next section and its benefits are outlined.

Two-stage Selection

A time-table of operations for two-stage selection in the second-generation is given in *Figure 1*. It is intended that the 200 unrelated full-sib families which constitute the second-generation breeding population will be represented by at least 200 progeny in each family, planted across two sites for security (*Fig. 1*). The field layout at each site will be randomised incomplete blocks with 40 trees in each block and single-tree plots (i.e. 40 sets of families in each block). The single-tree plots are to facilitate future collection of open-pollinated seed which should be suitable for the *stage-2* open-pollinated progeny testing (see subsequent discussion). Larger plots of say 50 to 100 trees would have the advantage of allowing more efficient selection of in-

June, year 1	PLANT 2nd GENERATION BREEDING POPULATION
	* population consists of 200 unrelated full-sib families.
	* 200 individuals in each family planted across two sites using a single-tree plot planting design.
Dec., year 8	MEASURE ALL TREES IN THE BREEDING POPULATION
Year 9	SELECT BEST 4 INDIVIDUALS FROM EACH FAMILY (STAGE-1 OF SELECTION)
	* selection is on an index combining phenotypic values.
	* scions and open-pollinated cones are collected from all 800 individuals selected at stage-1.
	* scion material used to establish clone banks.
	* open-pollinated seed sown in nursery.
June, year 10	OPEN-POLLINATED SEEDLINGS LIFTED FROM NURSERY AND PLANTED AS PROGENY TESTS ACROSS MULTIPLE SITES
Dec., year 14	MEASURE OPEN-POLLINATED PROGENY TESTS
Year 15	PROGENY TEST RESULTS USED TO SELECT BEST 2 OF EVERY 4 INDIVIDUALS FROM EACH FAMILY (STAGE-2 OF SELECTION)
June, year 15	SINGLE-PAIR MATINGS AMONG 400 INDIVIDUALS RETAINED AFTER STAGE-2 OF SELECTION
	* 'net merit index' used to pair parents.
	* mating is done in previously established clone banks.
Year 17	COLLECT CONTROLLED-POLLINATED CONES FROM CLONE BANKS AND SOW SEED IN NURSERY
June, year 18	PLANT 3rd GENERATION BREEDING POPULATION
	* population consists of 200 full-sib families.

Figure 1. — Time-table of operations for second-generation selection of radiata pine in South Australia.

dividuals within-families at *stage 1* (BURDON and SHELBORNE 1971), but seed collected from plots of this size would be largely full-sib or selfed and maybe unsuitable for progeny testing.

At *stage-1* of selection, four individuals having superior phenotypes are chosen from each of the 200 full-sib families in the breeding population (*Fig. 1*). This selection will be on a selection index combining phenotypic values for volume, stem straightness, branch quality and wood density. The phenotypic values are recorded for all progeny in the breeding population at 7½ years after planting (when the average height of trees should be about 14 m). The selection index would be calculated to achieve maximum possible gains in growth, straightness and branch quality, but as mentioned previously, a restriction will be imposed to hold the average level of wood density constant in the breeding population (i.e. restrictions detailed by COTTERILL and JACKSON 1981). This restriction would act mainly to prevent wood density from deteriorating due to negative genetic correlations between density and other traits included in the index, particularly volume (COTTERILL

and JACKSON 1981; DEAN *et al.* 1983).

Immediately following *stage-1* selection all of the four individuals chosen from each family are climbed to collect scion material and open-pollinated cones. The scions will be grafted onto seedling root stock to establish clone banks, while the open-pollinated seed is used without delay to establish open-pollinated progeny tests for *stage-2* of selection. The open-pollinated progeny tests are planted across multiple sites to allow selection for general adaptability to the breeding region.

Stage-2 of selection is based on results of a relatively early assessment (at 4½ years; *Fig. 1*) of the open-pollinated progeny tests for volume, stem straightness, branch quality, wood density and any malformations which may be apparent at that age (the average height of trees in the progeny tests should be 6 to 8 m). In every set of four parents tested, the two having the best general combining abilities (GCA's) are finally retained at *stage-2* to serve as parents for the next generation (i.e. *stage-2* selection to finally retain two out of every four individuals which were progeny tested per-family). GCA's would be determined by one of the least-squares procedures described in COTTERILL *et al.* (1983).

The 400 individuals finally retained after *stage-2* of selection (i.e. two individuals retained from each of the 200 full-sib families) will be crossed in a single-pair mating pattern to generate 200 new full-sib families which are planted out as the third-generation breeding population; some 17 years after the previous breeding population was established (*Fig. 1*). The single-pair matings are carried out in the clone banks which were established immediately after *stage-1* of selection and should have only just reached sexual maturity.

Two individuals are finally retained from each family after *stage-2*, instead of only one individual, because it creates a constant number of 400 parents for the breeding population of each generation and, of course, it achieves the previously recommended intensity of selection of one in 100. This constant number of breeding parents in each generation (chosen equally from each family) will greatly increase the effective size of the breeding population and reduce the rate of inbreeding (WRIGHT 1931).

COTTERILL and JAMES (1981) have outlined the theory of the two-stage selection used in this present breeding plan, and give genetic gains which can be expected under a wide range of circumstances. In a worked example for radiata pine in South Australia, these authors show that where selection is on a similar set of traits to those used in the present plan, two-stage selection can be expected to increase genetic gains by about 40% compared with a situation where only two out of 200 individuals are chosen from each family at *stage-1* and are retained for future breeding with no *stage-2* progeny test (i.e. the conventional within-family selection on phenotypic performance only). The advantage of the two-stage strategy is that it can achieve this additional genetic gain with little increase in the rate of inbreeding (because all selection is applied within-families) and no increase in generation time (because the *stage-2* progeny test is carried out while clone banks are maturing). The disadvantage of the strategy is that the progeny tests require additional labour.

It is worth mentioning that COTTERILL and JAMES (1981) also found little extra genetic gain was achieved by selecting any more than four individuals out of every 200 (i.e. selecting 2% at *stage-1*). These authors provide explana-

tions for this and other findings which would interest breeders who intend using two-stage selection.

Mating Pattern in the Breeding Population

The pattern of mating has an effect on genetic gains and rate of inbreeding in the breeding population (KIMURA and CROW 1963; KANG and NAMKOONG 1979, 1980; HOOD 1982), but its main influence is probably on gains from seed orchards (SQUILLACE 1973). Genetic gain, rate of inbreeding and, of course, economic cost have been the major considerations in choosing single-pair matings to regenerate the present breeding population. Other functions which are sometimes expected of the mating pattern, such as providing data to estimate GCA's, genetic parameters and realised gains (BURDON and SHELBOURNE 1971) were not considered. In the present plan these functions are served largely by open-pollinated progeny testing (as suggested by BURDON and SHELBOURNE 1971).

Single-pair mating requires only one cross per-parent and has the great advantage of being the least expensive and operationally the most simple of the controlled-pollinated mating patterns used in tree breeding (see reviews and discussion: SHELBOURNE 1969; BURDON and SHELBOURNE 1971; NAMKOONG 1979; TALBERT 1979). The fact that single-pair matings require so few crosses can, however, lead to reduced genetic gains. More elaborate mating patterns which require a number of crosses per-parent (e.g. the well known incomplete or disconnected half-diallels, disconnected factorials, or the new dodecahedron pattern devised by KRAUS 1982) have the disadvantage of being more costly and operationally complex. Nevertheless these patterns are able to generate a number of full-sib crosses within the progeny of each parent (i.e. full-sib families within half-sib families) and provide greater opportunity to increase genetic gains by selection among families (NAMKOONG 1979).

It has been mentioned previously that the amount of family selection which can be tolerated in the breeding population is strictly limited as far as long-term responses are concerned. Under diallel or factorial matings there is some opportunity for selection among the full-sib families within each half-sib relationship without greatly reducing the effective size of the breeding population (NAMKOONG 1979), but the intensity of this family selection would normally be low. Computer simulations by HOOD (1982) suggest that after five generations of selection in a breeding population, genetic gains under single-pair matings can be about the same as, or even greater than, gains under disconnected half-diallel matings.

Diallel or factorial matings can, as already mentioned, lead to greater genetic gains from seed orchards (i.e. greater gains in the plantations). The information that these mating patterns provide on specific combining (SCA) effects may be utilized directly when orchards are established from clones of parents which exhibited high SCA in crosses. More commonly, however, orchards would be established from a few (maybe 20 to 30) new selections made within only the very best families generated by the matings. In this case diallel or factorial matings, compared with single-pair matings, can substantially increase genetic gains from seed orchards by allowing more opportunity for selection among full-sib families before selecting best individuals from best families (see gain calculations of SQUILLACE 1973). Expressed another way, the diallel or factorial matings generate more families and therefore increase the family selection differential for selecting the

seed orchard population.

In the present breeding plan a 'net merit index' (ALLAIRE 1980) is employed to give single-pair matings a better probability of generating exceptional families, and increase the selection differential involved in choosing best families to provide best individuals for stocking seed orchards. Single-pair matings are usually conducted with more or less random pairing of parents, so that *parent 1* may happen to be crossed with a *parent 2*, 3×4 , and so on (certainly this is an assumption made in gain equations used by SQUILLACE 1973). The net merit index, in contrast to random pairing, attempts to achieve pair-combinations of parents which will maximise the 'net merit' or net economic value of families which are generated by single-pair matings. The index works by estimating the net merit of the 'expected progeny' of each potential pair-combination of parents, assuming that the contributions from each parent are additive (ALLAIRE 1980). This net merit is essentially the average (or mid-parent value) of a potential pair of parents GCA's for multiple-traits, weighted to reflect the relative economic importance of changes in each trait. Pair combinations having the highest net merit would be mated (with certain limitations on mating relatives; discussed later).

The net merit index has not been used previously in tree breeding and its potential to provide additional gains from orchards is, for the moment, unproven. The success of the net merit index in predicting performance of parents in crosses would depend partly on having a high proportion of additive to non-additive variance in the population (ALLAIRE 1980; GORDON 1980). WILCOX *et al.* (1975) have reported fairly high ratios of GCA : SCA for radiata pine in New Zealand, although these estimates are for only a limited sample of parents. No estimates of GCA : SCA ratios are available for radiata pine in South Australia, but it is encouraging for the future success of mating under net merit index that exceptional full-sib families in existing progeny trials often prove to be combinations of parents having superior GCA's. The net merit index may be especially usefull in increasing genetic gain where non-linear relationships exist between economic value and changes in particular traits (discussed by ALLAIRE 1980). If non-linear economic relationships are found to exist for certain traits, which seems likely, then there will be a strong argument for not only using the net merit index to pair parents, but also to actually select parents at *stage-2* of the two-stage selection (i.e. selection of individuals on their expected net merit in crosses; ALLAIRE 1980).

By using the net merit index to pair best parents with best parents (i.e. positive assortative mating) or to pair parents with complementary characteristics (i.e. complementary or 'corrective mating'; ALLAIRE 1980) it may be possible to develop a nucleus of elite individuals either within or outside the breeding population which would supply most of the material for stocking orchards. "(Or under clonal forestry; an elite nucleus to generate outstanding full-sib families for mass propagation)". This is similar to the concept of 'open nucleus breeding' in animal improvement (JACKSON and TURNER 1972; JAMES 1977), and its potential in tree breeding deserves closer examination than is possible in this article.

A policy of mating unrelated individuals (i.e. 'maximum avoidance' of inbreeding; KIMURA and CROW 1963) will be adopted for the first and second generations of the present breeding plan. By the time the third generation arrives,

more information should be available on the consequences of inbreeding in radiata pine, and strategies designed to alleviate these consequences (i.e. sublining) may be better proven. If necessary, sublining can still be implemented in the third generation. 'Circular' or 'cousin' matings (KIMURA and CROW 1963; COCKERHAM 1970; NAMKOONG 1979) have been proposed for reducing inbreeding in later generations of the breeding population. However, these mating patterns seem to be of little practical value since they can take 500 generations or more to achieve even a slight advantage in levels of inbreeding (KIMURA and CROW 1963). Evidence also suggests that diallel or factorial matings offer no advantage in reducing inbreeding (KANG and NAMKOONG 1979, 1980; HOOD 1982).

Selection for the Seed Orchard Population

It has been mentioned previously that open-pollinated progeny tests and clone banks are established immediately after *stage-1* of the two-stage selection, and the progeny tests are first measured at 4½ years to facilitate an early *stage-2* selection. The plan is then to measure these open-pollinated progeny tests again at 7½ years, and to use the results of this later and more reliable assessment to choose the 20 most superior individuals of those selected at *stage-1*. Cuttings will be collected from these 20 individuals in the clone bank and used without delay to establish new seed orchards. It would be ideal if the 20 individuals were unrelated (at least in early generations) but this would not be imposed as a restriction on selection. The calculations of SQUILLACE (1973) suggest that genetic gains from seed orchards can be improved by stocking those orchards with the best available material, despite the fact that some of the material might be related.

The selection of individuals to stock orchards would normally be on the same traits as those selected for in the breeding population. It is not intended to cull orchards and they would be eventually clear-felled as newer orchards came into production.

The opportunity exists to convert each of the open-pollinated progeny tests into a seedling seed orchard after the 7½ year assessment. Indeed, in the future this type of seedling orchard may be used instead of clonal orchards. SHELBOURNE (1969), SQUILLACE (1973) and SILEN and WHEAT (1979) comment on the potential of seedling orchards as a source of improved seed.

Introducing New Genetic Material

There is no doubt that breeders in the future will want to introduce new genetic material into the breeding population. However, a distinction has to be made here between adding the promising genotypes from other breeding programs and introducing new genetic variability (new genes), from say the gene pool, into the entire breeding population. The former can be achieved by obtaining scions or pollen from the outstanding individuals, and then simply using each individual as a parent in single-pair matings employed to regenerate the breeding population.

The task of replenishing genetic variability in the entire breeding population is much more difficult to achieve (OSMAN and ROBERTSON 1968). MORTON (1979) describes a reticulate mating pattern which can be used to introduce particular attributes, of a few otherwise inferior individuals, into the breeding population but supposedly without lowering the performance of the more improved population. However, these reticulate matings require two generations to complete. A combination of selection and back-

crossing (OSMAN and ROBERTSON 1968) may be the only practical solution for more quickly getting new attributes from the gene pool, or some other population, into the breeding population. Crossbreeding would have to be resorted to when the attributes required from breeding were not available in the species.

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