

GLOVER, N.: Variation among provenances of *Gliricidia sepium* (Jacq.) WALP. and implications for genetic improvement. – Proc. of a Workshop sponsored by Nitrogen Fixing Tree Association, Hawaii. 168–173 (1987). — GUPTA, A. K. C., DWIVEDI, A. K. and PADMINI SHIVKUMAR: Forest tree improvement programmes in Uttar Pradesh. Indian For. **118**(6), 389–393 (1992). — HAZARA, C. R. and TRIPATHI, S. B.: Soil properties, micro meteorological parameters, forage yield and phosphorus uptake of berseem as influenced by phosphorus application under Agroforestry system of production. J. Agron. Crop. Sci. **156**, 145–152 (1986). — HUNT, R.: Basic growth analysis. Academic division, Unwin Hyman Limited, London. 112 (1990). — International Seed Testing Association: Rules for seed testing and evaluation. Seed Sci. Tech. **13**(2), 356–513 (1976). — KADAMBI, K.: Silviculture and management of teak. School of Forestry, Stephen F. Austin State University, Texas. 137 pp. (1972). — KAOSA-ARD, A.: Teak: Its natural distribution and related factors. Nat. Hist. Bull. Siam. Soc. **29**, 55–74 (1981). — KEOGH, R. M.: Teak (*Tectona grandis* LINN. F.) provisional site classification chart for the Caribbean, Central America, Venezuela and Columbia. For. Ecol. Manage. **4**, 143–153 (1982). — KERTADIKARA, A. W. S. and PRAT, D.: Genetic structure and mating system in teak (*Tectona grandis* L.F.) provenances. Silvae Genet. **44**(2–3), 104–110 (1995). — KOZLOWSKI, T. T.: Water supply and tree growth. Part I- Water deficits. For. Abst. **43**(2): 57–95 (1982). — LARSEN, H. S., SOUTH, D. B. and BOYER, J. M.: Root growth potential, seedling morphology and bud dormancy correlate with survival of loblolly pine seedlings planted in December in Alabama. Tree Physiol. **1**(3), 253–263 (1986). — LEBOT, V.: Genetic improvement of exotic broad leaved species in Madagascar. Bois et Forests des Tropiques **247**, 21–36 (1996). — MAGUIRE, D. A., SCHRUDER, G. F. and MUSTAFA SHAIKH.: A biomass yield model for high density *Acacia nilotica* plantation in Sind, Pakistan. For. Ecol. Manage. **37**(4), 285–302 (1990). — MANOJKUMAR: Genetic divergence, Isozyme pattern and micropropagation studies in sandal (*Santalum album* L.). M.Sc. Thesis, Tamil Nadu Agricultural University, Coimbatore (1994). — PARAMATHMA, M.: Studies on genetic inheritance in interspecific crosses of Eucalyptus. Ph.D. Thesis, Tamil

Nadu Agricultural University, Coimbatore (1992). — RAI, R. S. V., KRISHNASWAMI, S. and SRINIVASAN, V. M.: Juvenile and adult performance of six species of Eucalyptus and selection index for seedling index for seedling quality. Indian J. For. **5**, 259–262 (1982). — RAJESH, N., ASHOKAN, P. K. and BABU, L. C.: Influence of water stress on the physiological and biometrical parameters of selected forest species. Proceedings of 9th Kerala Science Congress held at Thiruvananthapuram, January 1997. pp. 61–66 (1997). — RAO, C. R.: Advanced Statistical Methods in Biometric Research. John Wiley and Sons, Inc., New York. 390 pp. (1952). — RITCHIE, G. A.: Carbohydrate reserves and root growth potential in Douglas fir seedlings before and after cold storage. Can. J. For. Res. **12**, 905–912 (1982). — SINGH, N. B. and CHAUDHARY, V. K.: Multivariate analysis of genetic divergence in wild apricot (*Prunus armeniaca* LINN.). Indian J. For. **15**(3), 211–216 (1992). — SNEDECOR, G. W. and COCHRAN, W. G.: Statistical methods. 6th ed. Oxford and IBH Publishing Co., New Delhi. p. 507 (1967). — SUBRAMANIAN, K. N., GOVINDARAJ, P. and SASIDHARAN, K. R.: Provenance trial in *Eucalyptus grandis* and its implications to forestry programmes. Silvae Genet. **41**(4–5), 239–242 (1991). — SUBRAMANIAN, K. N., NICODEMUS, A. and RADHAMANI, A.: Teak improvement in India. Forest Genetic Resources **22**, 33–36 (1994). — TEWARI, D. N.: Biodiversity and forest genetic resources. International Book Distributors, Dehra Dun, India. 329 pp. (1994). — VENKATESH, C. S., KOSHY, M. P., CHACKO, K. C. and INDIRA, E. D.: Genetic improvement of teak in Kerala. Kerala Forest Research Institute Research Report No. 13, 4–21 (1986). — WAKELEY, P. C.: In: Proceedings of Forest Genetics – short course. North Carolina State University, Raleigh. June 1959 (1959). — WHITE, K. J.: Research results: a selection of annotated references of Teak (*Tectona grandis* L.F.). Occasional Paper, Forestry Research Support Programme for Asia and Pacific, No. 19, 22 pp. (1993).

A Nucleus Breeding Plan for Radiata Pine in Australia

By T. L. WHITE¹), A. C. MATHESON²), P. P. COTTERILL³), R. G. JOHNSON⁴), A. F. ROUT⁵) and D.B. BOOMSMA⁵)

(Received 16th January 1998)

Abstract

The Southern Tree Breeding Association Inc. (STBA), consisting of 20 private companies and government agencies working cooperatively to breed improved varieties of radiata pine (*Pinus radiata*) for Australia, has adopted the concept of a nucleus breeding strategy entailing a total breeding population of 300 selections subdivided into two components: a nucleus population (which receives more emphasis in terms of breeding and testing and consists of the best 10% or so of the population) and a main population consisting of the remainder of the

breeding population. This paper describes and compares three different plans for operational implementation of a nucleus breeding strategy by the STBA. The first option (Option 1) is the simplest entailing open-pollinated management of the main population and unified nucleus and main populations. The second two plans (Options 2a and 2b) employ complementary mating designs with pollen-mix management of the main population and a breeding population (consisting of the main and nucleus populations) that is further sub-divided into three unrelated lines. These lines serve as unrelated breeding groups to manage inbreeding in the deployment population. Options 2a and 2b differ only in the use of seedlings (Option 2a) or rooted cuttings (Option 2b) in unreplicated full-sib family plots used for within-family selection. The three options are compared in terms of costs, logistics, and detailed genetic gains predictions. In general, costs are similar for all three options and relatively small when compared with the overall STBA budget. Similarly, all three options are logistically feasible given the staffing and resources of the STBA. Thus, comparison of genetic gains represents the most meaningful criterion for deciding among the three options and in this regard, both Options 2a and 2b are clearly superior to Option 1. This is largely due to the pollen-mix management of the main population and the use of

¹) School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA

²) CSIRO Forestry and Forest Products, PO Box E4008, Kingston, Canberra, ACT 2604, Australia

³) C/- CSIRO Forestry and Forest Products, PO Box E4008, Kingston, Canberra, ACT 2604, Australia

⁴) USDA Forest Service, Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA

⁵) Southern Tree Breeding Association, PO Box 1811, Mount Gambier, SA 5290, Australia

well-replicated progeny tests to estimate GCA. The use of rooted cuttings in Option 2b adds significantly to the length of the cycle (from 12 to 14 years), but also results in more genetic gain per breeding cycle. An Appendix providing additional details of assumptions and calculations is available from the authors.

Key words: breeding strategy, genetic gain, radiata pine, costs and benefits, nucleus breeding.

Introduction

Interest in advanced-generation breeding for forest trees has been increasing in recent years as breeding programs approach second and third generations of breeding. A number of plans have been proposed (e.g., SHELBOURNE, 1969; TALBERT, 1979; VAN BULJTENEN and LOWE, 1979; BURDON and NAMKOONG, 1983; MATHESON and BROWN, 1983; NAMKOONG *et al.*, 1980; SKRØPPA, 1982; COTTERILL, 1984; SHELBOURNE *et al.*, 1986; WHITE *et al.*, 1993), many dealing with mating designs or population structure rather than the details of the plan itself. A number of plans have been proposed for breeding radiata pine in different parts of Australia (BUTCHER, 1985; ELDRIDGE, 1987; PEDERICK, 1987; COTTERILL and CAMERON, 1989; JOHNSON, 1989, 1990). Genetic gain calculations as a basis for comparison are few (COTTERILL, 1986), because gains themselves depend on the almost infinitely variable details of the strategy.

COTTERILL (1986) compared gains from ten breeding plans as applied to *P. radiata* and found that simpler schemes with shorter cycle times tended to produce greater gains per decade than more complex ones with longer cycle times that produce more gain per generation. In particular, single-pair mating with combined index selection produced more gain per decade than half-diallel mating with combined index selection. In a later paper COTTERILL *et al.* (1988) introduced the concept of nucleus breeding to forestry. The essence of this scheme, originally used in sheep breeding (JAMES, 1977, 1978; HOPKINS, 1978), is that most effort is expended on the most promising genetic material (the nucleus population) and less effort is expended on less promising genetic material (the main population). In addition to allocating effort appropriately, nucleus breeding provides early profitability for the breeding program via the fast-moving nucleus.

The Southern Tree Breeding Association (STBA) consists of 20 private companies and government agencies working co-operatively to breed radiata pine for Australia. COTTERILL (1984) described early plans for breeding radiata pine in South Australia, and these formed the basis of STBA plans. In 1989, STBA adopted the concept of a nucleus breeding strategy for radiata pine and determined that the breeding population is to consist of approximately 300 members including the nucleus and main populations. Important features (see COTTERILL and CAMERON, 1989) aimed at maximizing genetic gain per unit time are: (1) a small nucleus (containing 10% or so of the total members of the breeding population) receiving most emphasis in the program, (2) a main population receiving less emphasis, (3) use of index selection, (4) two-way transfer of material between nucleus and main populations, and (5) assortative, complementary and best-mate mating of nucleus members.

While a nucleus strategy was endorsed in concept in 1989, the STBA had yet to adopt a breeding plan detailing how a nucleus strategy would be implemented on an operational basis. To ensure that all efforts of the next cycle of improvement are maximally efficient, the STBA needed to develop and adopt a complete working plan for the radiata pine breeding program that describes the nature, timing and costs of all breeding and testing efforts.

This paper describes and compares three different plans (options) for operational implementation of a nucleus breeding strategy by the STBA. The first is the simplest implementation of the COTTERILL *et al.* (1988) strategy and the other two are similar modifications of it. The three options are compared in terms of logistics, general features and detailed genetic gains predictions. So that these comparisons would be valid, it was necessary for us to specify completely all details for one complete cycle of breeding and testing. We believe it is undesirable to make firm plans more than one cycle into the future because of changing technologies and markets (cf. KANG, 1979); however, if desirable, each of the plans described herein could be repeated for many cycles as a breeding plan based on recurrent selection for general combining ability.

Description of Breeding Plan Options

The starting point for developing breeding plan options was the nucleus strategy outlined by COTTERILL *et al.* (1988) and COTTERILL and CAMERON (1989) and described below as Option 1. Due to the value of simplicity (COTTERILL, 1986), no modification to this strategy was seriously considered if it either significantly increased the generation interval (by greater than two years over Option 1) or if it appreciably increased either costs or logistical complications. After detailed comparisons of costs and logistics and rudimentary calculations of genetic gains (WHITE *et al.*, 1992a) and discarding many alternative options, we settled on two alternative options plus the original option for comparison (the original plan, labeled Option 1, and Options 2a and 2b).

Option 1: Single Main Population Managed by Open Pollination; Single Nucleus.

This option follows the original ideas for nucleus breeding outlined by COTTERILL and CAMERON (1989) and elsewhere (COTTERILL *et al.* 1988; COTTERILL, 1989). General features are: (1) A single nucleus and a single main population so that inter-mating is permitted among all members within each population (i.e., there are no substructures such as sibs or multiple populations), (2) The nucleus population is maintained by controlled pollination and (3) The main population is maintained by open-pollination with 50% thinning from below in the open-pollinated progeny tests at age 4.5 years.

Nucleus Population

The nucleus population in Option 1 contains 30 members (i.e., parents) intermated to create 130 control-pollinated (CP) families (Figure 1). Best-mate indices (COTTERILL and DEAN, 1990) and complementary mating (COTTERILL and CAMERON, 1989) are used to choose the crossing pattern among all 30 members. There is no restriction on the crossing pattern except that crosses among relatives are avoided to preclude inbred progeny.

The 130 CP families are planted in well-designed trials with 20 individuals per family planted on each of 5 trial locations giving a total of 13,000 progeny. The trials perform seven functions: (1) rank the 30 nucleus members for general combining ability (GCA), (2) rank the 130 CP families for operational deployment, (3) estimate genetic parameters needed for selection index development, (4) select 22 or 23 individuals (using combined index selection) to form 75% of the next generation's (i.e., generation $n+1$) nucleus population (the other 25% comes from the main population), (5) select 30 individuals to form 10% of the $n+1$ generation's main population, (6) mate together the 22 or 23 next generation nucleus selections (used as both male and female parents) and (7) collect OP cones from the 30 $n+1$ generation main population selections for the following generation progeny trials. Matings among relatives that would

GENERAL FEATURES

DESCRIPTION OF FEATURES

Nucleus Population

Size	30 selections	Members chosen by index selection.
Structure	Unified	Complete intermating allowed; related matings avoided.
Breeding	130 CP families	130 CP families by mate-index and complementary breeding.
Testing	13,000 progeny	20 CP seedlings per family on each of 5 test locations.
Cycle Length	12 years	

30 selections
to main

7.5 selections
to nucleus

Two-way gene flow

Main Population

Size	300 selections	Members chosen by index selection.
Structure	Unified	Complete intermating allowed among members in progeny tests.
Breeding	300 OP families	OP seed collected from progeny tests each generation.
Testing	30,000 progeny	33 OP seedlings per family x 300 fams x 3 test sites; 50% thin at 4.5 yrs.
Cycle Length	12 years	9 years if not synchronized with nucleus; 12 years if synchronized.

Figure 1. – General features of Option 1: Unified main and nucleus populations with open-pollinated management of main population. CP = control pollinated; PM = pollen mix; OP = open pollinated.

enhance gains from functions 4 and 5 above are generally avoided because the resulting inbreeding depression would impair functions 1, 2 and 3.

The entire cycle requires 12 years to complete (see Table 1 for details) assuming: (1) two years to complete crossing in the previous generation's progeny tests (i.e., no clone banks), (2) two years for cone development, (3) one year to grow the seedlings in the nursery and (4) 6.5 years for the tests to reach selection age. The next cycle would begin in the following year (cycle year 13) with crossing in the progeny tests on the next generation selections.

Main Population

The main population in Option 1 contains 300 members (i.e., parents) each generation, maintained by collecting open-pollinated (OP) seed from each of 300 selections (Figure 1). The 300 families are planted in three progeny test locations with an average of 33.3 individuals per family at each location giving a total of 30,000 progeny. The six functions of these trials are: (1) rank the 300 members of the main population for GCA, (2) estimate genetic parameters needed for selection index develop-

ment, (3) select 7 or 8 individuals to form 25% of the n+1 generation nucleus population, (4) select 270 individuals to form 90% of the n+1 generation main population, (5) mate together the 7 or 8 n+1 generation nucleus selections and (6) collect OP cones from the 270 n+1 generation main population selections for the next cycle of progeny tests.

The 30,000 progeny in trials are thinned from below to 15,000 progeny (i.e. a 50% thinning) to enhance the genetic quality of the pollen cloud. It is assumed, for the purposes of estimating costs, that this does not require an extra formal measurement at age 4.5 years.

It is possible to complete a cycle of breeding and testing in 9 years for the main population. However, the cycle length for the nucleus is 12 years and it is not clear how to manage nucleus and main populations not in synchrony because of the two way gene flow each generation (Figure 1). So the length of the main population cycle is also assumed to be 12 years. Thinning, assessment and selection could be carried out two years later with consequent improvements in precision and genetic gain from older tests, and greater assurance of open-pollinated cones on all selected trees.

Option 2: Co-structured Nucleus and Main Populations; Polymix Managed Main

Options 2a and 2b both employ co-structured nucleus and main populations (Figure 2), are identical for the main population, and differ for only one feature for the nucleus population (described below). General features of both 2a and 2b are: (1) use of three different selection indices to create three different lines or varieties, MP (multi-purpose), DG (wood density and growth) and GP (growth and resistance to *Phytophthora*), (2) a nucleus of 40 members divided into three unrelated subdivisions ("MP", "DG" and "GP"), (3) a co-structured main population subdivided into the same three lines as the nucleus, (4) two-way gene flow between nucleus and main populations within a line, (5) no gene transfer between different lines except for developing material for deployment to operational plantations, (6) forced inbreeding to increase gains in the nucleus, (7) polymix management of the main population, (8) use of unreplicated family block plots called selection and breeding facilities, SBFs, that are used both for within-family selection and breeding and therefore obviate the need for breeding clone banks.

Nucleus Population

The MP nucleus contains twice as many parents (20) as the other two lines, because there are twice as many traits being bred (growth, stem straightness, branch quality and *Dothistroma*-resistance). The nucleus populations for the DG and GP lines have 10 parents each.

There are three types of crosses made as part of nucleus breeding each generation (Figure 2): 50 control-pollinated (CP) crosses among members between lines to determine which are best for operational deployment (called deployment crosses and not shown in Figure 2), 100 CP crosses made among members

of the same line for making next-generation selections (called SBF crosses because they are to be carried out in selection and breeding facilities), and 40 polymix (PM) crosses for estimating GCA of the 40 nucleus members. These three types of crosses have quite different objectives and hence different mating and trial designs described below. However, the overall philosophy is similar to reciprocal recurrent selection or line breeding used for agricultural crops (ALLARD, 1960). The additive genetic value of each line is improved by within-line breeding, while between-line crosses (deployment crosses) are made for operational deployment.

The 50 deployment CP crosses and 40 PM crosses, combined with up to 10 controls (i.e. 100 families), are planted in well-designed trials (hereafter called GCA tests) on 10 locations with 20 seedlings per family at each location giving 2,000 seedlings per location. The five objectives of these trials are: (1) rank the 50 deployment crosses for operational deployment in that generation, (2) rank the 40 members of the nucleus for GCA, (3) estimate genetic parameters from the 40 PM crosses for use in the family portion of selection indices, (4) determine the importance of specific combining ability (SCA) in between-line combining ability by examining whether mid-parent values of the 40 nucleus members (based on GCAs) accurately rank the 50 deployment crosses, (5) make selections within the 40 PM crosses for the next generation main and/or nucleus populations.

In both Options 2a and 2b, the 100 CP crosses planted in SBFs are made by crossing among members within each nucleus line and consist of both outcrosses and related matings. In Option 2a, offspring are planted in large unreplicated blocks of 120 seedlings of each family or could be planted in 2 blocks of 60 seedlings per family separated by some distance as insurance against catastrophic loss. In Option 2b, offspring are propagat-

Table 1. – Timing and activities for the 12-year cycle of Option 1 characterized by a single nucleus population and a single main population maintained by open-pollination (see Figure 1).

Cycle Year	Calendar Year	Activities for the Nucleus Population	Activities for the Main Population
1	1991	Begin crossing to form 130 CP fams	1. Make selections 2. Collect cones if available
2	1992	Complete crossing	1. Collect cones from remaining selections 2. Sow seed in nursery
3	1993	Collect cones from year 1 crosses	Plant tests on 3 locations
4	1994	1. Collect cones from year 2 crosses 2. Sow seed in nursery	No activities; tests are 1-year-old
5	1995	Plant tests on 5 locations	No activities; tests are 2-years-old
6	1996	Weed control on 5 test locations	No activities; tests are 3-years-old
7	1997	No activities; tests are 2-years-old	Thin poorest 50% in all 3 tests
8	1998	No activities; tests are 3-years-old	No activities; tests are 5-years-old
9	1999	No activities; tests are 4-years-old	Prune tests to facilitate measurements
10	2000	No activities; tests are 5-years-old	1. Measure tests at 6,5-years-old 2. Make selections ^a
11	2001	Prune tests to facilitate measurements	No activities
12	2002	1. Measure tests at 6,5-years-old 2. Make selections 3. Collect pollen for cycle 2 crossing	No activities unless measurement and selection in main population are delayed for synchrony with nucleus

^a) Measurement and selection in main tests could be delayed to cycle years 11 or 12.

GENERAL FEATURES

DESCRIPTION OF FEATURES

Nucleus Population

Line	MP	DG	GP	
Size	20	10	10	40 total selections in 3 disconnected (unrelated) lines.
Breeding for:				
1. SBFs	50	25	25	100 total CP fams (with related & selfs) planted in SBFs.
2. PM tests	20	10	10	40 polymix crosses for GCA PM tests on 10 locations.
Testing in:				
1. SBFs	6000	3000	3000	100 CP fams with 120 seedlings (Opt. 2a) or cuttings (Opt. 2b) per SBF plot.
2. PM tests	4000	2000	2000	40 PM fams x 20 seedlings per fam x 10 test locations = 8,000 seedlings.
	↓ ↑	↓ ↑	↓ ↑	Two-way movement; 25% of each nucleus from main; 13% of each main from nucleus.

Main Population

Line	MP	DG	GP	
Size	150	75	75	300 total members in main population; 160 used as females; up to 300 males.
Breeding:				
1. In pollen mix	<150	<75	<75	Pollen mix for each line composed from selections bearing pollen.
2. PM families	80	40	40	160 PM fams created on best selections also bearing female flowers.
Testing in:				
1. PM tests	8000	4000	4000	160 PM fams x 20 seedlings per fam x 5 test locations = 16,000 seedlings.
2. SBFs	4000	2000	2000	160 PM fams x 50 seedlings per fam in each SBF plot = 8,000 seedlings.

Figure 2. – General features of Options 2a and 2b: Three co-structured main and nucleus population lines with selection and breeding facilities (SBFs) for both nucleus and main and pollen-mix management of the main. CP = control pollinated; PM = pollen mix; SBF = unreplicated family blocks to be used to make within-family selection and subsequent breeding. Note 50 deployment crosses planted in the nucleus PM tests are not shown (at 200 trees per family, this means 10,000 more trees planted in the nucleus PM tests); they do not contribute to the gains calculations, but were included in cost estimates.

ed vegetatively so that the SBFs are formed from 4 rooted cuttings of each of 30 seedlings per family laid out as family blocks. This is the only difference between Options 2a and 2b.

Both Options 2a and 2b call for 100 CP family plots x 120 individuals per plot giving a total of 12,000 trees. The five objectives of the SBFs are: (1) select 30 individuals (out of 12,000) to form 75% of the next generation's nucleus population, (2) select 40 individuals to form 13% of the next generation's 300-member main population, (3) mate together the 30 n+1 generation nucleus population selections, (4) mate together the 40 n+1 generation main population selections and (5) estimate genetic parameters for the within-family portion of the selection index.

Timing of events and details of activities are shown in table 2. Use of rooted cuttings adds an extra 2 years to the cycle length (14 years vs 12 years).

Main Population

Options 2a and 2b are identical for the main population which contains 300 members as in Option 1. The main population is subdivided into the same three lines as is the nucleus (i.e. MP, DG and GP). Relatives may exist in main and nucleus populations within a line, but not between lines. The MP main line has twice as many members (150) as the other two lines for the same reason as the corresponding nucleus populations (i.e. more traits in MP).

The main population is managed by controlled pollinations using three pollen mixes, each mix composed of pollen from all members within a line. The amount of pollen from each male parent in the mix is affected by availability of pollen, the availability of male strobili and the member's breeding value (LINDGREN, 1986; LINDGREN and MATHESON, 1986). Members not producing female strobili will contribute more pollen because

pollen is the only way they become part of the breeding population.

Twice as many polymix (PM) families are created in the MP line compared with the other two lines such that 80 of the better members (i.e. higher ranking) from the 150 in the MP line are used as females to form 80 PM families and 40 PM families are formed similarly in each of the other two lines. Choice of females in the formation of PM families is based on high breeding value, presence of female strobili and acceptably few relatives in the nucleus and female group of that line.

These 160 PM families are planted in two complementary test designs. First, 20 seedlings from each family are planted in randomized, replicated designs at each of 5 locations giving 3,200 seedlings per location and a total of 16,000 seedlings in replicated trials. The five functions of these replicated trials are: (1) rank the members of each line for GCA, (2) estimate genetic parameters for the family portion of the selection index

used in the main population, (3) make a portion of the selections for the next generation's main population, (4) collect pollen to form the next generation's pollen mixes for the main population, and (5) mate together selections (if convenient).

The second portion of PM seed from each of the 160 PM families is used to establish a single plot of 50 seedlings for each family (or 2 separated plots of 25 trees each to protect against catastrophic loss). These must be conveniently situated for breeding. These 160 plots are the SBFs and have five functions: (1) make the remainder of the selections for the next generation's main population, (2) make 10 selections to form 25% of the next generation's nucleus population, (3) collect pollen for the next generation's pollen mixes for the main population, (4) conduct PM mating on those selections chosen as females to form the next generation's main population, and (5) conduct mating to form PM and CP crosses on the 10 selections moved up to the next generation's nucleus.

Table 2. – Timing of activities for the 12-year cycle of Option 2a and the 14-year cycle of Option 2b (see Figure 2). Main population activities are identical for both options, nucleus activities apply to both options unless noted.

Cycle Year	Calendar Year	Activities for the Nucleus Population	Activities for the Main Population
1	1991	Begin crossing: 100 CP fams for SBFs, 50 CP fams for deployment, and 40 PM fams for GCA tests ^c	1. Form 3 pollen mixes: 1 per line 2. Begin crossing for 160 PM fams
2	1992	Complete crosses	Complete crosses
3	1993	Collect cones from year 1 crosses	Collect cones from year 1 crosses
4	1994	1. Collect cones from year 2 crosses 2. Sow seed for GCA tests ^c & SBFs	1. Collect cones from year 2 crosses 2. Sow seed for GCA tests and SBFs
5	1995	1. Plant GCA tests on 10 locations ^c 2 ^a . Plant 120-tree fam. blocks (SBFs) 2 ^b . Line-out seedlings for rooting	1. Plant GCA tests on 5 locations ^c 2. Plant 50-tree family plots (SBFs)
6	1996	1 ^a . No activities; Tests are 1-year-old 1 ^b . Set 10 cuttings per seedling	No activities; Tests are 1-year-old
7	1997	1 ^a . No activities; Tests are 2-years-old 1 ^b . Plant SBFs of cuttings	No activities; Tests are 2-years-old
8	1998	1 ^a . No activities; Tests are 3-years-old 1 ^b . Repeat; Plant SBFs of cuttings	No activities; Tests are 3-years-old
9	1999	No activities; Tests are 4 ^a and 2 ^b yrs	No activities; Tests are 4-years-old
10	2000	No activities; Tests are 5 ^a and 3 ^b yrs	No activities; Tests are 5-years-old
11	2001	1. Prune GCA tests at age 5.5 years 2 ^a . Prune SBFs; 2 ^b . SBFs are 4-yrs-old	Prune GCA tests and SBFs
12	2002	1. Measure GCA tests 2 ^a . Measure SBFs and make selections 3 ^a . Collect pollen for next cycle	1. Measure GCA tests and SBFs 2. Make selections 3. Collect pollen for next cycle
13 ^b	2003	1 ^b . Prune SBFs at age 5.5 years	(Main is completed in year 12)
14 ^b	2004	1 ^b . Measure SBFs and make selections 2 ^b . Collect pollen for next cycle	

^a) Applies to Option 2a only. ^b) Applies to Option 2b only.

^c) Nucleus GCA tests are the same for Options 2a and 2b: 10 locations with 100 families (50 CP families for deployment, 40 PM families for GCA testing of the 40 nucleus parents and 10 controls). Main GCA tests consist of 160 PM families on each of 5 locations.

^d) Each SBF of Option 2b contains 120 plants from a single CP family: 4 ramets from each of 30 seedlings.

Within-family selections are made both in SBFs and in the replicated progeny trials. However, logistics will probably determine that most of the 160 selections to be used as females for the main PM families will come from the SBFs. Pollen may come with equal ease from either trial type. The cycle length for the main population of Options 2a and 2b is 12 years (Tables 2 and 3), but could be extended to 14 to retain synchrony with Option 2b.

Methods of Comparing the Breeding Plan Options

Genetic gains, logistics and costs were assessed for each of the several options originally considered. Genetic gain calculations were made along similar lines to COTTERILL and CAMERON (1989) using the gain estimation formula of NEWTON TURNER and YOUNG (1969) and COTTERILL (1986):

$$\Delta G = ih^2 J\sigma_p \quad (1)$$

where $J = [(1-M)/(1-N) + M(M-N)/(N(1-N))]^{1/2}$

$$M = [1 + (q-1)r]/q$$

$$N = [1 + (q-1)rh^2]/q$$

and

q = family size used to calculate family heritability,

r = average genetic correlation among family members,

h^2 = heritability on an individual tree basis,

i = standardized selection intensity and

σ_p = phenotypic standard deviation on a tree basis.

Each generation, gain in the nucleus (G_N) derives partly from selections from the previous generation's nucleus and partly from selection in the main population (moved up to the nucleus and hereafter called an "admixture" to the nucleus). Similarly, gain in the main population (G_M) is partly derived from selection in the main population itself and partly from selection in the nucleus moved down to the main. These effects of two way gene flow were accounted for using the approach of COTTERILL and CAMERON (1989):

$$G_N = (1-x)G_{NN} + xG_{NM} - xZ \quad (2)$$

$$G_M = (1-y)G_{MM} + yG_{MN} + yZ$$

where G_{NN} is gain in the nucleus from selections made in the nucleus,

G_{NM} is gain in the nucleus from selections made in the main,

G_{MM} is gain in the main from selections made in the main,

G_{MN} is gain in the main from selections made in the nucleus.

x is the proportion of nucleus parents derived from the main,

y is the proportion of main parents derived from the nucleus, and

Z is the difference in mean breeding values between nucleus and main.

For making gain calculations, the only trait considered was basal area with the following assumptions (COTTERILL and DEAN, 1990): individual-tree heritability (h^2) is 0.2 with a phenotypic standard deviation (σ_p) of 50 cm²; and the original mean of the entire breeding population is 170 cm² which is a

Table 3. – Genetic gain components, genetic gains, and costs from three options for nucleus breeding of radiata pine in Australia. Option 1 has 1 line and seedlings; Option 2a has 3 lines and seedlings, Option 2b has 3 lines and cuttings.

Option	Length (yrs)	Genetic Gain Components (%) ^a				Genetic Gain ^b (%)		Genetic Advantage Above Unimproved Population ^c (%)		Costs Per Cycle (\$)	
		G _{MM}	G _{MN}	G _{NN}	G _{NM}	After 1 Cycle	After 1 Decade	After 1 Cycle	After 1 Decade	Nominal	PV ^d
Option 1										182,700	132,100
Main	12	8.4	20.9	N/A	N/A	11.1	9.3	9.6	8.0		
Nucleus	12	N/A	N/A	24.5	11.8	17.5	14.6	31.3	26.1		
Option 2a										191,400	132,000
Main	12	16.8	21.0	N/A	N/A	19.4	16.1	17.8	14.8		
Nucleus	12	N/A	N/A	24.0	22.4	19.8	16.5	33.5	28.2		
Option 2b										206,600	142,200
Main	14	16.8	23.9	N/A	N/A	19.7	14.1	18.2	13.0		
Nucleus	14	N/A	N/A	27.6	22.4	22.5	16.1	36.3	25.9		

^a) G_{MM} = gain from selections made in the main and used there; G_{MN} = gain from selections made in the nucleus and moved to the main; G_{NN} = gain from selections made in the nucleus and used there; G_{NM} = gain from selections made in the main and moved to the nucleus.

^b) Genetic gain values for the nucleus population (G_N) and main population (G_M) are expressed as a percentage above the mean starting value of 170 cm².

^c) The advantage values are the mean breeding values in either the main or nucleus populations after one generation of breeding expressed as a percentage above the starting value of 170 cm². These advantage values reflect the genetic gain (see footnote b above) added to the initial starting breeding value of the main (167.4) or nucleus (193.4).

^d) Present value.

weighted average of the 10% of the population in the nucleus (with mean = 193.4 cm²) and 90% of the breeding population in the main (with mean = 167.4 cm²): $170 = 0.1 \times 193.4 + 0.9 \times 167.4$. With these assumptions, the starting difference in mean breeding value between the nucleus and main populations is $Z = 26$ cm². All calculations were conducted in the units of measure (cm²) and converted to percentages at the final step.

While this approach to estimating genetic gains is convenient for purposes of calculation, it was not possible to account for all aspects of the options. Thus, specific simplifying assumptions were made to allow use of this approach. These assumptions are described generally here and detailed in an Appendix (available from the authors). Calculations for Option 1 assume no foreign pollen contamination of main OP progeny trials by pollen of below average breeding value. The thinning at age 4.5 is assumed to have equal heritability as at age 6.5 (even though the tests are younger and not actually measured before thinning). Further the genetic correlation between age 4.5 and 6.5 is assumed to be 1.0. Finally, the thinning is assumed not to affect the precision of the family means calculated at age 6.5 (i.e., family means calculated at age 6.5 based on 50% of the trees have the same precision as family means calculated from all trees). Thus, this method is likely to overestimate genetic gains for Option 1.

There are several aspects of Options 2a and 2b which could not easily be incorporated into the formulae. Each of these would increase genetic gains from Option 2, but are ignored in the calculations. Thus, estimated gains for Option 2 are conservative, because no allowance in the gains calculations was made for: 1) known deployment of outcrosses by intermating between lines in Option 2 compared to possible deployment of inbreds from the single unified nucleus of Option 1; 2) within-family selection from a single uniform plot (family blocks within SBFs); 3) increased selection intensity by selecting some female parents from outside the SBFs (such as in the GCA tests with PM crosses); 4) testing families as cuttings rather than as seedlings (Option 2b would enhance gain for a program deploying cuttings); 5) optimizing the genetic value of the pollen mix by inclusion of greater quantities of pollen from parents with higher breeding values (LINDGREN and MATHESON, 1986); 6) use of forced inbreeding to rid the population of negative deleterious alleles (STRICKBERGER, 1968; LINDGREN and GREGORIUS, 1976; HALLAUER and MIRANDA, 1981; VAN VLECK *et al.*, 1987; NAMKOONG *et al.*, 1989); and 7) additional gains from using three different selection indices (for the MP, DG, GP lines) in a multi-trait breeding program (NAMKOONG, 1976; NAMKOONG *et al.*, 1989, pp. 72, 97).

Costs and logistics for each option were assessed by charting the exact yearly activities (Tables 1 and 2). At each step, operational realities were considered. For example, for all seedling plantings, it was assumed that twice the amount of seed would need to be sown to yield the desired number of plantable seedlings. For rooted cuttings, it was assumed that 10 cuttings had to be set to yield four plantable cuttings. Similar levels of buffering were assumed for each activity in order, as much as possible, to simulate the actual costs of implementing these strategies. Logistics were then determined by assessing the yearly workload in light of the staffing and resources of the STBA.

The costs included in the economic analyses were those representative of incremental or variable costs associated with each of the different options. These costs included travel, labor, supplies and equipment for all of the breeding and testing activities: seedling production, planting of tests, weed control at year 1, pruning of trees prior to each assessment, measure-

ment costs, thinning (Option 1), and all breeding and seed processing costs. Costs such as for land, site preparation, salaries of the main STBA staff and overhead were not included in the analyses but rather considered as constant costs that would be incurred for any breeding plan. Thus, this is not a complete economic analysis, but rather a comparison of the marginal costs associated with the different options.

After the costs of each activity were estimated, these were aggregated for the period of the cycle length in two different ways. First, the costs of each option were summed on a nominal basis (simply summing the costs for each activity for the period). Second, the present value of all costs was calculated by first discounting all costs to 1991 using a 5% real interest rate and then summing the discounted costs. Care must be exercised when comparing options spanning different lengths of time (12 years for Options 1 and 2a, 14 years for Option 2b). The STBA could begin another cycle of breeding and testing 2 years earlier for the shorter options, but it is impossible to predict the exact form (and hence the costs) of the next cycle of strategies. Thus, we have chosen to aggregate all costs on a "per cycle" basis for this current cycle. If the overall economic value of the next cycle of breeding and testing is positive, then this approach may slightly under value Options 1 and 2a relative to 2b because the value of starting the next cycle 2 years earlier is not directly accounted for.

Finally, in future breeding cycles the costs of breeding will be reduced because crossing will be conducted in the family plots (in SBFs) located close to operational facilities. In the current cycle, the STBA will incur the higher costs associated with travelling to the various field test and seed orchard locations to collect pollen and make controlled crosses. For the purpose of costing the various options, we compromised and assumed that one year of crossing was conducted according to the current STBA situation (higher travelling and associated costs), while the second year was in SBFs (with lower costs) that would be in place at the end of the current cycle. This assumption has only a minor impact on cost comparisons among the options.

Results of Comparisons of Gains and Costs

Genetic gains for basal area after one generation under Option 1 (original nucleus plan with unified main and nucleus populations and OP management of the main) were predicted as 17.5% for the nucleus and 11.1% for the main population (Table 3). Use of polycross management of the main population approximately doubles the gain contribution of selections made in the main population to both the nucleus ($G_{NM} = 22.4\%$ vs. 11.8%) and the main population ($G_{MM} = 16.8\%$ vs. 8.4%). Overall, this polycross management of the main results in substantially more gain in the main population (19.4% and 19.7% for Options 2a and 2b) compared with Option 1 (11.1%). This implies continued enhancement of nucleus gains in subsequent generations of breeding resulting from better material being moved up from the main.

In addition to examining genetic gains, it is useful to compare the three options in terms of mean breeding values of the nucleus and main populations after one generation of improvement (Table 3). Consisting of the top 10% of the breeding population, the nucleus begins the breeding cycle with a higher mean breeding value for basal area (193.4 cm²) than does the main (167.4 cm²). After adding the gains from one generation of improvement to these starting values, the mean breeding values of the nucleus and main can be expressed as the advantage (in %) above the starting value of the entire, unimproved breeding population (170 cm²). There is substantial superiority of the nucleus above the main population for all three options

examined, illustrating the value of nucleus breeding strategies. For example for Option 2a, after one cycle of breeding, the nucleus mean breeding value is 33.5% above the unimproved starting population, while the main population is only 17.8% better than unimproved.

In the nucleus, use of cuttings (Option 2b) compared with seedlings (Option 2a) in the unreplicated family blocks (in SBFs) increases gain from 19.8% per cycle to 22.5% (Table 3). This cuttings option also increases gain in the main population slightly (19.7% vs. 19.4%), because selections made in the nucleus and moved down to the next generation's main population are predicted to be of higher genetic quality due to their selection in nucleus SBFs composed of cuttings (i.e. $G_{MN} = 23.9\%$ vs. 21.0% for Options 2b and 2a, respectively).

While gains for Option 2b exceed those for Option 2a when expressed on a per cycle basis, the reverse is true when gains are expressed on a per unit time basis. Option 2a has slightly higher gain for the nucleus (16.5% per decade vs. 16.1% respectively) and substantially higher for the main (16.1% per decade vs. 14.1%). Thus, the increase in cycle length of 2 years (from 12 to 14 years) required to implement the use of cuttings in the nucleus SBFs offsets the increased gains per cycle achieved by this option.

The costs of completing these three options are very similar when considered in the context of the entire STBA budget for this Australia-wide tree improvement cooperative (Table 3). On a nominal dollar basis (in which all costs are simply summed for the entire cycle, at 1992 dollars), the costs range from \$182,700 (Option 1) to a high of \$206,600 (Option 2b). If this difference between the most and least expensive options is expressed on an annual basis, the difference is less than \$2,000 per year which is less than 1% of the annual STBA operating budget. Any other comparisons of costs (e.g., comparing Option 2a to Option 1 or making comparisons on a present value basis instead of a nominal basis), makes the differences even smaller. Thus, the differences in costs between any of these options are so small that cost should simply not be a consideration when choosing between options. Even small differences in gain between options would result in large financial gain considering that the improved material will be deployed over most of the radiata pine plantation estate in Australia.

Finally, it is important to compare the logistics of each option to ensure that the plan is really achievable as conceived. While charting the activities of each option on an annual basis (Tables 1 and 2), we examined the complexity of completing each task given the organizational structure and capabilities of the STBA. All three of the options can, with high probability, be completed as planned. The total number of trees planted (the most costly aspect since it implies measuring each planted tree) is 43,000 for Option 1 (13,000 nucleus plus 30,000 main, Figure 1) and 56,000 for Options 2a and 2b (32,000 nucleus plus 24,000 main, Figure 2). Neither of these amounts is too large for a nation-wide cooperative breeding organization conducting an entire generation of breeding. For example, the database of 106 progeny tests used to predict breeding values of the 1,200 first-generation radiata pine selections in Australia contained over 275,000 trees (WHITE *et al.*, 1992b).

Discussion

The original nucleus breeding strategy proposed by COTTE-RILL and CAMERON (1989) and represented here by Option 1, contained some important concepts for tree breeding: 1) a small nucleus (containing 10% or so of the total members in the breeding population) which receives the most emphasis in the program, 2) a main population receiving less emphasis, 3) use

of index selection, 4) two-way transfer of material between the main and nucleus populations, and 5) best-mate mating designs for CP crossing of the nucleus selections. However, there could be problems implementing Option 1 for STBA: 1) the best selections may not have female flowers or pollen at age 4.5 (time of thinning and pollination in the OP progeny tests of the main population), 2) costs and logistics of pollinating on 7-year-old nucleus selections located in 5 diverse CP test locations are high, 3) safety laws may eventually preclude controlled-pollination on the ortets, 4) the nucleus would quickly become inbred with no way of alleviating inbreeding depression in material deployed to operational plantations, and 5) open-pollinated management of a radiata pine main breeding population relying on pollination at 4.5 years could mean substantial losses of genetic gain due to foreign pollen entering from outside the OP progeny tests.

Thus, the important concepts from the original plan were retained in Options 2a and 2b, but in addition some new features were added to enhance genetic gain in the nucleus and main populations and to increase the logistical flexibility during breeding and deployment. The genetic gain calculations developed using Equations 1 and 2 were not flexible enough to account for the total benefits of these enhancements and we deliberately tried to make conservative assumptions such that the gains for Options 2a and 2b are probably underpredicted relative to those for Option 1. For this reason, the rationale behind each modification made to the original nucleus strategy is described below.

Co-Structured Nucleus and Main Populations in Three Unrelated Lines

Division of the breeding population into three unrelated lines serves two distinct functions. First, the lines serve as multiple populations (BURDON and NAMKOONG, 1983; NAMKOONG *et al.*, 1989, p. 71) so that different selection indices (one for each line) are used as opposed to one general index (NAMKOONG, 1976). This will enhance the gains for high wood density in the DG line and probably for growth overall (because growth is the first or second most important trait in three different indices each of which contains fewer traits than one overall index).

Second, the three lines permit maintenance of some control on pedigree (material from different lines is always known to be unrelated), so that concern about build up of relatedness in the nucleus is less of a problem. Crosses between lines will always be outcrossed regardless of the inbreeding coefficient within a line. In this regard, the lines are serving as sublines or breeding groups being used in other tree improvement programs to control inbreeding in the deployment population (VAN BULJTENEN, 1976; BURDON *et al.*, 1978; KANG, 1979; VAN BULJTENEN and LOWE, 1979; McKEAND and BEINEKE, 1980; PURNELL and KELLISON, 1983; COGGESHALL and BEINEKE, 1986; CARSON *et al.*, 1990; McKEAND and BRIDGWATER, 1992; WHITE *et al.*, 1993).

Because inbreeding within lines will be removed in deployment crosses under Option 2, forced inbreeding within each line can be used to increase gains. Forced inbreeding coupled with selection can be used to increase gains by removing deleterious recessive alleles from the breeding population (STRICKBERGER, 1968, p. 747; LINDGREN and GREGORIUS, 1976; HALLAUER and MIRANDA, 1981; VAN VLECK *et al.*, 1987, p. 217; NAMKOONG *et al.*, 1989, p. 57). In the nucleus the STBA will be making crosses among related selections and also making selfs, but the gains from this use of forced inbreeding were not accounted for in any gains calculations.

Some of the gains achieved from using three different selection indices (one for each line) will be lost during deployment, because lines will not have been selected for all traits. For example, some gains in wood density will be lost when making deployment crosses between the DG and MP line if the MP line has not been bred for high density. In the current strategy, the MP (multi-purpose) line has emphasis on several traits and growth rate is emphasized in all three lines. Thus, losses of gain may not be as great as they first appear. Another option to overcome this problem is to breed all lines for all traits (e.g. CARSON *et al.*, 1990; WHITE *et al.*, 1993). The STBA may also eventually adopt this approach.

Polymix Testing for GCAs of Both the 40 Nucleus and the Main Population

We believe that precise breeding value predictions are critically important for the 40 nucleus members because these are the selections that will be used for making crosses deployed to operational plantations. It is always better statistically to replicate these GCA tests as widely as possible (WHITE and HODGE, 1992), and this is especially important for a nationwide cooperative such as the STBA because material will be deployed to plantations spanning a wide range of climates and soil types.

Further, because of the historical independence of the members' testing activities prior to joining the STBA, most selections have not been tested together in an orthogonal manner on the same test locations. Thus, for both the main and nucleus selections, it is important to develop precise breeding value predictions.

Polymix testing (Options 2a and 2b) increases precision of ranking of the 40 nucleus members, and hence genetic gain, because PM tests are on 10 test locations compared to the CP tests of Option 1 which are on 5 locations (*Figures 1 and 2*). It is much less expensive and logistically easier to replicate 40 PM families across 10 locations rather than 130 CP families.

Precision of the rankings of the nucleus and main selections will increase in future generations as ancestral data is accumulated through polymix testing. Because the PM tests do not have to be used for breeding work as in Option 1, the PM tests can remain undisturbed and be measured past age 6.5 (say to half or more of rotation). The data from older ages will be important for assessing juvenile-mature relationships and for use as ancestral data for ranking future nucleus selections. These measurements will be less expensive on 40 PM compared with 130 CP families for the nucleus.

Precision of the breeding value predictions in both the nucleus and main populations is also increased because of the large number of males in the pollen mix of Option 2. Pollen mix progeny testing is not always optimal (BURDON and VAN BUIJTENEN, 1990), but it is generally quite efficient for ranking selections (BURDON and SHELBOURNE, 1971; LINDGREN, 1978; VAN BUIJTENEN and NAMKOONG, 1983; VAN BUIJTENEN and BRIDGEWATER, 1986; BURDON and VAN BUIJTENEN, 1990; BRIDGEWATER, 1992). In the nucleus especially, relatedness among selections will increase in future generations meaning that best-mate crosses among nucleus selections will undoubtedly be between relatives. Thus, the 130 CP families of Option 1 will suffer varying levels of inbreeding depression making the rankings of the nucleus members less precise from the CP tests compared with PM families with a large sample of males.

The PM tests add another source of material for selection. While most breeding will be conducted in the SBFs for logistical ease, selections can also be made in the PM tests. Pollen can be collected from selected individuals to make up the pollen mixes (main and nucleus) of the next generation and

pollination can be conducted on outstanding individuals. This was not accounted for in the gains calculations for Options 2a and 2b.

Use of Selection and Breeding Facilities (SBF)

Complementary mating designs have been adopted by several tree improvement programs to separate and maximize the efficiency of two different objectives (VAN BUIJTENEN, 1976; VAN BUIJTENEN and LOWE, 1979; LOWE and VAN BUIJTENEN, 1986; McKEAND and BRIDGEWATER, 1992; WHITE *et al.*, 1993). The replicated PM tests described above meet the first objective of efficiently ranking the selections in both the main and nucleus populations. Then, unreplicated (or replicated only for insurance against catastrophic loss) plots containing trees from a single family are used to meet the second objective of making outstanding forward selections (i.e. within-family selections). We call these plots selection and breeding facilities (SBFs), because they can also serve a third function, that of breeding (i.e. they are the places where controlled-pollinations are made.)

Use of SBFs increases the gain from within-family selection. All offspring from a given family that are candidates for selection are planted in a single plot (or perhaps 2 different plots). Then, the best candidate for selection is compared directly against its siblings (as opposed to being planted in several different blocks on several test sites). Selection index theory assumes that correction for test and block effects is perfect, when in fact the adjustments must be estimated.

The logistics of breeding are greatly enhanced through use of SBFs, and costs are decreased. The SBFs are set up specifically to be on field site locations near operational facilities. Thus, costs and time for controlled-pollinations will be reduced compared to pollinating in more remote field locations where selections are made or in clone banks. Although the design of the SBFs (all progeny from a given cross in one location) slightly increases the risk of loss from fire (offset by their being close to operational facilities) it also reduces costs.

SBFs allow the use of forced inbreeding to increase gains from selection. The SBFs are not used to rank parents, thus balance (number of seedlings per plot, etc) and varying levels of inbreeding depression are not a concern. So, crossing among relatives is promoted. The use of related crosses will increase gains and does not have to be avoided.

The number of seed required from each family can vary when SBFs are used. In the nucleus for example, the CP seed is not planted in replicated field tests as it is in Option 1, rather PM seed is used for that purpose. The CP seed in Option 2 is planted only in SBFs which are used solely for within-family selection and breeding. Thus, the large numbers of CP seed needed to ensure balance of field tests in Option 1 (200 seed per family for 100 plantable seedlings) is not required. In Option 2, each SBF may contain a different number of offspring. This may reduce the number of years and costs of completing the same number of CP crosses. However, for simplicity in our calculations, we have assumed that each family has the same representation in SBFs.

Use of Cuttings in the Nucleus Selection and Breeding Facilities

The use of cuttings can increase gain from within-family selection compared with use of seedling plots (SHELBOURNE, 1992). The weakest aspect of within-family selection is that each genotype is unreplicated (represented on a single microsite). Using the average of 4 ramets of each seedling to rank the seedlings from within a given family, increases the precision of the ranking and therefore the gain from selection (see SHELBOURNE, 1992 and our calculations in the Appendix – available from the authors).

Some STBA members will use cuttings for operational deployment. If cuttings are actually being planted operationally, then the fact that the final selections have been made on the basis of performance as cuttings increases the gain compared with selection of seedlings (because the correlation between cutting and seedling performance is unlikely to be 1). The reverse would be true for organizations actually deploying seedlings; gain would be less if selection were based on cutting performance. We did not account for this in the gains calculations i.e. we assumed no c-effects.

The logistics of breeding seem much easier when cuttings are used. There will be 4 cuttings and the original hedged seedling available for controlled-pollination on any selection (both those chosen to form the next nucleus and those moving down to the main). The hedged seedling can be managed later for flower and pollen production. Compared to crossing on a single seedling (as in Options 1 and 2a), the crossing should be less costly and more easily completed in the proposed time.

The extra 2 years needed to complete Option 2b compared to the seedling Option 2a is a serious disadvantage, and our preliminary calculations (detailed in the Appendix, available from the authors) indicate that the extra time is not justified by enough extra gain (Table 3). However, in different situations (such as in the next generation when most STBA members may be actively deploying cuttings), we believe that SHELBOURNE's (1992) concept of cloning the breeding population may prove quite useful.

Combined Testing of the 40 PM Families, 50 Deployment Families and 10 Controls

Both Options 2a and 2b call for 50 single pair crosses (called deployment families) to be made between lines; all other crosses are made within lines each generation. These deployment crosses are intended to represent the very best material that could be deployed that generation. Because these top 50 families are tested on 10 sites (compared with 5 sites in Option 1), precision of ranking on the top 50 deployment families will be increased. Thus, STBA members planning to deploy bi-parental families from CP seed will know which ones have performed well across a wide range of site types and climates.

The principal disadvantage of all nucleus options considered is that there are no rankings developed for specific CP crosses that could be used to choose the best specific crosses for operational deployment. This is an important disadvantage only if significant specific combining ability (SCA) exists. If SCA is not important, then deployment crosses are accurately chosen by using the mid-parent of the GCAs developed from the PM tests. Because PM and deployment crosses are tested together on the same 10 test locations under Option 2, the importance of SCA can be assessed experimentally. If SCA is not important, then the rankings of the 50 full-sib deployment families should be sufficiently accurately predicted by the mid-parent breeding values obtained from the PM performance of the 40 parents.

The 10 controls included in these tests will provide an important test of realized gains against the best material in the STBA program. The realized gains should nearly reflect gains expected from operational deployment options.

General Discussion and Conclusions

Gains from either Option 2a or 2b are greater than those of Option 1. These extra gains come primarily from use of polymix crosses in the main and nucleus populations and the use of family blocks for within-family selection (SBFs). Division of both main and nucleus populations into three lines under Option 2 has the extra advantage of eliminating inbreeding in

trees used for deployment. Further, use of these three lines can address multiple breeding objectives and costs much the same as a unified breeding population. Finally, replication of the PM and deployment crosses in the nucleus across 10 sites will pay dividends for deployment because the STBA members will have very precise rankings on the economically most important material in the program. If genotype x environment interactions are important, the breeding value predictions used for deployment can be tailored to specific types of deployment sites (WHITE and HODGE, 1989, p. 157).

With rapidly evolving technologies, we believe that it is appropriate to plan ahead for only one generation of breeding and testing (cf KANG, 1979); however, each of the three options considered here could conceivably be used for multiple generations of breeding; and it is always important to consider population sizes. The population sizes employed (30 to 40 in the nucleus and 300 in the main) are large enough to sustain substantial genetic gains for many generations (see review by WHITE, 1992), and in addition there is a wealth of other genetic material of radiata pine not included in the current breeding population that could be infused in future generations. Much of this material could conceivably be of excellent genetic quality and comes from three distinct sources: 1) material being bred and tested by STBA members that was out of phase (too young) and could not be included when the current breeding population was being assembled, 2) provenances and families that are being tested in a wide variety of gene conservation and genetic tests around Australia, and 3) material that could be potentially obtained from other radiata pine breeding programs around the world (for example, Chile, JAYAWICKRAMA and BALOCCHI, 1993; and New Zealand, CARSON *et al.*, 1990).

Acknowledgements

This work would not have been possible without the support of the members of the Southern Tree Breeding Association. We thank JOHN CAMERON, PETER VOLKER, GREG DUTKOWSKI and SUE JARVIS for the stimulating discussions and reviews.

References

- ALLARD, R. W.: Principles of Plant Breeding. Wiley, NY (1960).
- BRIDGE-WATER, F. E.: Mating designs. In: Handbook of Quantitative Forest Genetics. Eds. L. FINS, S.T. FRIEDMAN and J.V. BROTSCHOL. Kluwer, Boston. pp. 69–95 (1992).
- BURDON, R. D. and NAMKOONG, G.: Multiple populations and sublines. *Silvae Genet.* **32**: 221–222 (1983).
- BURDON, R. D. and SHELBOURNE, C. J. A.: Breeding populations for recurrent selection: Conflicts and possible solutions. *N.Z.J.For.Sci.* **1**: 174–193 (1971).
- BURDON, R. D., SHELBOURNE, C. J. A. and WILCOX, M. D.: Advanced selection strategies. In: Proc. Third World Consultation on Forest Tree Breeding. March 1977, Canberra, Australia. pp. 1133–1147 (1978).
- BURDON, R. D. and VAN BUIJTENEN, J. P.: Expected efficiencies of mating designs for reselection of parents. *Can. J. For. Res.* **20**: 1664–1671 (1990).
- BUTCHER, T. B.: A plan for breeding radiata pine in Western Australia. Internal Report, Dept. Conserv. and Land Management, Perth, Australia. 62 p. (1985).
- CARSON, M. J., BURDON, R. D., CARSON, S.D., FIRTH, A., SHELBOURNE, C. J. A. and VINCENT, T. G.: Realizing genetic gains in production forests. In: Proc. IUFRO S2.02–05 Douglas-fir, Lodgepole pine, Sitka spruce and *Abies* spp. August, Olympia, WA (1990).
- COGGESHALL, M. V. and BEINEKE, W. F.: The use of multiple breeding populations to improve northern red oak (*Quercus rubra* L.) in India. In: Proc. IUFRO Conf. on Breeding Theory, Progeny Testing and Seed Orchards. Oct. 13 to 17, Williamsburg, VA. pp. 540–546 (1986).
- COTTERILL, P. P.: A plan for breeding radiata pine. *Silvae Genet.* **33**: 84–90 (1984).
- COTTERILL, P. P.: Genetics gains expected from alternative breeding strategies including simple low cost options. *Silvae Genet.* **35**: 212–223 (1986).
- COTTERILL, P. P.: The nucleus breeding system. In: Proc. Twentieth South. For. Tree Improve. Conf. June, Charleston, SC. pp. 36–42 (1989).
- COTTERILL, P. P. and CAMERON, J. N.: Radiata pine breeding plan. Tech. Rep. 89/20. APM Forests Pty. Ltd., Victoria, Australia. 50 p. (1989).
- COTTERILL, P. P. and DEAN, C. A.: Successful Tree Breeding with Index Selection. CSIRO Div. Forestry, Canberra, Australia. 80 p. (1990).
- COTTERILL, P., DEAN, C., CAMERON, J. and BRINDBERGS, M.: Nucleus breeding: a new structure for rapid improvements under clonal forestry. In: Breeding Tropical Trees: Population structure and genetic improvement strategies in clonal and

seedling forestry. Eds. GIBSON, G. L., GRIFFIN, A. R. and MATHESON, A. C. OFI, Oxford, UK and Winrock, Arlington. pp. 39–51 (1988). — ELDRIDGE, K. G.: Southern Tree Breeding Association 1987 Working Plan. Unpublished report. CSIRO (1987). — HALLAUER, A. R. and MIRANDA, J. B.: Quantitative Genetics in Maize Breeding. Iowa State Univ. Press, Ames (1981). — HOPKINS, I. R.: Some optimum age structures and selection methods in open nucleus breeding schemes with overlapping generations. *Anim. Prod.* **26**: 267–276 (1978). — JAMES, J. W.: Open nucleus breeding systems. *Anim. Prod.* **24**: 287–305 (1977). — JAMES, J. W.: Effective population size in open nucleus breeding schemes. *Acta. Agric. Scand.* **28**: 387–392 (1978). — JAYAWICKRAMA, K. J. S. and BALOCCHI, C.: Growth and form of provenances of *Pinus radiata* in Chile. *Aust. For.* **56**: 172–178 (1993). — JOHNSON, G. R.: STBA's Nucleus Population: A Proposal for the Breeding Population Structure. Tech. Rep. 90–01. STBA, Mt. Gambier, Australia. 22 p. (1990). — JOHNSON, I. G.: The Breeding Strategy for Radiata Pine In New South Wales. Tech. Pap. 47. New South Wales Forestry Commission, Sydney, Australia. 58 p. (1989). — KANG, H.: Long-term tree breeding. In: Proc. 15th South. For. Tree Improve. Conf. June 19 to 21, Starkeville, Miss. pp. 66–72 (1979). — LINDGREN, D.: Genetic gain by progeny testing as a function of mating design and cost. In: Third World Consultation on Forest Tree Breeding. March 21 to 26, Canberra, Australia. pp. 1223–1235 (1977). — LINDGREN, D.: How should breeders respond to breeding values? In: Proc. IUFRO Conf. Breeding Theory, Progeny Testing and Seed Orchards. October 13 to 17, Williamsburg, VA. pp. 361–372 (1986). — LINDGREN, D. and GREGORIUS, H. R.: Inbreeding and coancestry. In: Proc. IUFRO Adv. Gen. Breeding. June 1976, Bordeaux, France. pp. 49–65 (1976). — LINDGREN, D. and MATHESON, A. C.: An algorithm for increasing the genetic quality of seed from seed orchards by using the better clones in higher proportions. *Silvae Genet.* **35**: 173–177 (1986). — LOWE, W. J. and VAN BULJTENEN, J. P.: The development of a sublining system in an operational tree improvement program. In: Proc. IUFRO Conf. on Breeding Theory, Progeny Testing and Seed Orchards. Oct. 1986, Williamsburg, VA. pp. 98–106 (1986). — MATHESON, A. C. and BROWN, A. G.: Radiata pine breeding Manual (CSIRO Division of Forest Research, Canberra). (1983). — MCKEAND, S. and BEINEKE, F.: Sublining for half-sib breeding populations of forest trees. *Silvae Genet.* **29**: 14–17 (1980). — MCKEAND, S.E. and BRIDGEWATER, F.E.: Third-generation breeding strategy for the North Carolina State University-Industry Cooperative Tree Improvement Program. In: Proc. IUFRO, Resolving Trop. For. Resource Concerns Through Tree Improv., Gene Conserv., and Domestication of New Species. October, Cali, Colombia. pp. 234–240 (1992). — NAMKOONG, G.: A multiple-index selection strategy. *Silvae Genet.* **25**: 199–201 (1976). — NAMKOONG, G. H., BURLEY, J. and BARNES, R. D.: A philosophy of breeding strategy for tropical forest trees. Tropical Forestry Paper No. 16. Commonwealth Forestry Institute, Oxford. 67 pp. (1980). — NAMKOONG, G., KANG, H. and BROUARD, J. S.: Tree Breeding: Principles and Strategies. Springer-Verlag, New York, NY. 175 p. (1989). — NEWTON TURNER, H. and YOUNG, S. S. Y.: Quantitative Genetics in Sheep Breeding. Macmillan, Melbourne, Australia (1969). —

PEDERICK, L. A.: A Plan for Breeding Radiata Pine by the Department of Conservation, Forests and Lands. Res. Rep. 38. Dept. Cons., Forests and Lands, Melbourne, Australia. 50 p. (1987). — PURNELL, R. C. and KELLISON, R. C.: A tree improvement program for southern hardwoods. In: Proc. 17th South. For. Tree Improve. Conf. June 7 to 9, Athens, GA. pp. 90–98 (1983). — SHELBOURNE, C. J. A.: Tree breeding methods. In: For. Res. Inst. Tech. Pap. 55. New Zealand For. Serv., Wellington, NZ. 45 p. (1969). — SHELBOURNE, C. J. A.: Genetic gains from different kinds of breeding population and seed or plant production population. *South African Forestry Journal* **160**: 49–66 (1992). — SHELBOURNE, C. J. A., BURDON, R. D., CARSON, S. D., FIRTH, A. and VINCENT, T. G.: Development plan for radiata pine breeding. New Zealand Forest Serv., Rotorua, NZ. 142 p. (1986). — SKRØPPA, T.: Breeding strategies with Norway spruce in southeastern Norway. In: Proc. IUFRO Conf. Breeding Strategies Including Multiclonal Varieties. Sensenstein, West Germany (1982). — STRICKBERGER, M. W.: Genetics. The Macmillan Co., London, GB. 868 p. (1968). — TALBERT, J. T.: An advanced-generation breeding plan for the N.C. State University-Industry pine tree improvement cooperative. *Silvae Genet.* **28**: 72–75 (1979). — VAN BULJTENEN, J. P.: Mating designs. In: Proc. IUFRO Joint Meeting on Advanced Generation Breeding. June, Bordeaux, France. pp. 11–27 (1976). — VAN BULJTENEN, J. P. and BRIDGEWATER, F.: Mating and genetic test designs. In: Advanced Generation Breeding of Forest Trees. Southern Coop. Series Bull. 309. Louisiana Ag. Exp. Stn., Baton Rouge, LA. pp. 5–10 (1986). — VAN BULJTENEN, J. P. and LOWE, W. J.: The use of breeding groups in advanced generation breeding. In: Proc. 15th South. For. Tree Improve. Conf. June 19 to 21, Starkeville, Miss. pp. 59–65 (1979). — VAN BULJTENEN, J. P. and NAMKOONG, G.: Mating designs. In: Progeny Testing of Forest Trees. South. Coop. Series Bull. No. 275. Texas A&M Univ., College Station, TX. pp. 7–13 (1983). — VAN VLECK, L. D., POLLAK, E. J. and OLTENACU, E. A.: Genetics for the Animal Sciences. W. H. Freeman and Co., New York, NY. 391 p. (1987). — WHITE, T. L.: Advanced-generation breeding populations: Size and structure. In: Proc. IUFRO Conf. Breeding Tropical Trees. Oct., Cali, Colombia (1992). — WHITE, T. L. and HODGE, G. R.: Predicting Breeding Values with Applications in Forest Tree Improvement. Kluwer Academic Pub., Dordrecht, The Netherlands. 367 p. (1989). — WHITE, T. L. and HODGE, G. R.: Test designs and optimal age for parental selection in advanced-generation progeny tests of slash pine. *Silvae Genet.* **41**: 293–302 (1992). — WHITE, T. L., HODGE, G. R. and POWELL, G. L.: Advanced-generation breeding strategy for slash pine in the southeastern United States. *Silvae Genet.* **42**: 359–371 (1993). — WHITE, T. L., MATHESON, A. C., BOOMSMA, D. B. and ROUT, A. F.: Logistics, costs and genetic gains of five options of nucleus breeding strategies. STBA Tech. Rep. 92–01. Southern Tree Breeding Association, Mt. Gambier, South Australia. 38 p. (1992a). — WHITE, T. L., ROUT, A. F., BOOMSMA, D. B. and DUTKOWSKI, G. W.: Predicted breeding values for 1213 first-generation parents. STBA Tech. Rep. 92–02. Southern Tree Breeding Association, Mt. Gambier, South Australia. 27 p. (1992b).

Genetic Mapping of Quantitative Trait Loci Underlying Complex Genotype-Phenotype Relationships in Forest Trees

By R. WU¹⁾²⁾³⁾ and Y. HAN²⁾

(Received 25th September 1998)

Abstract

The complex relationship between genotype and phenotype can be attributed to individual quantitative trait loci (QTLs).

¹⁾ Forest Biotechnology Group, Department of Forestry, Box 8008, North Carolina State University, Raleigh, NC 27695-8008, USA

²⁾ Research Institute of Forestry, Chinese Academy of Forestry, Beijing 100091, China

³⁾ Corresponding to the current address:

RONGLING WU, Program in Statistical Genetics, Department of Statistics, Box 8203, North Carolina State University, Raleigh, NC 27695, USA

Tel: (919)-515-1932

Fax: (919)-515-7315

E-mail: rrwu@statgen.ncsu.edu

These underlying QTLs are often complex in terms of their statistical and biological properties. They could be pleiotropic, linked, developmentally or environmentally plastic, and interacting. Statistical methods have been developed to map QTLs and proven to be successful in detecting QTLs of large effects on the phenotype. Yet, these are not vastly adequate, because the application of these methods is limited by the complex nature of QTLs. In this review, we outline recent developments of statistical methods for mapping these complex QTLs within the framework of composite interval mapping. In each section, we discuss the statistical model for dealing with a key topic, followed by computational algorithms. The topics discussed include mapping pleiotropic QTLs for multiple quantitative traits, QTLs linked on the same chromosome, development-