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A Breeding Strategy for the New Zealand Radiata Pine Breeding Cooperative

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Abstract

This paper documents the breeding strategy of the New Zealand Radiata Pine Breeding Co-operative (NZRPBC) following a revision in 1997 to 1999. This co-operative serves 15 members in New Zealand and south-eastern Australia, and provides improved genetic material used for planting throughout New Zealand and in parts of Australia. In the revised strategy, emphasis on recurrent selection for general combining ability (GCA), a 2-superline structure, main population and breeds are maintained. A non-regionalised breeding programme, and a final selection around age eight years are also maintained. A new Structural Timber breed is to be formed, along with a Clear Cuttings breed (with modified emphases compared to the long-standing Long Internode breed). The Growth and Form breed will be expanded, recombining new superior parent clones. The existing Dothistroma-resistant breed will also be progressed, while the existing Long Internode and High Wood Density breeds will be used as sources of selections. Good parents not selected for the breeds will be used in the main population. A Guadalupe breeding population is also to be established.

The combined populations are to have a census number near 550 and a target status number of 400. The role of the breeds is to get optimum genetic gain while delaying the build-up of inbreeding, and to be the main source of new selections for seed orchards. The main population will serve as a reservoir of genetic diversity, as a source of candidates for existing and future breeds, and as a form of 'genetic insurance'. Candidates within breeds will be crossed in disconnected factorials and tested as seedlings or as clones within families. Candidates within the main and Guadalupe population will be tested as seedlings.

The previous full review of the New Zealand breeding strategy for radiata pine was in 1986. The strategy was revised because of subsequent developments that impacted on breeding, including: new information and new tested parents; adopting a collaborative government-industry approach to breeding; advances in breeding strategy, forest genetics and propagation techniques; and changes in emphases and practices in the forestry sector. The 1986 strategy had several key results, namely an emphasis on recurrent selection for general combining ability, a 2-superline breeding population with relatedness kept within superlines, stratifying the breeding population to an unspecialised main population and specialised breeds (with some overlap), a single breeding programme for all New Zealand, and separate crossing for recombination and for estimation of GCA.

Key words: breeding strategy, *Pinus radiata,* New Zealand, Australia, breeding population, breeds, main population, superlines, multiple populations.

Introduction

Radiata pine (*Pinus radiata* D. DON) is the main plantation forestry species in New Zealand and Australia, with a combined planted area of 2.2 million hectares (Anonymous, 1997a, 1998). It is successfully grown on a wide range of sites (soil type, latitude, elevation and rainfall) in these two countries. The distribution of major plantings of radiata pine in New Zealand and south-eastern Australia are shown in LAVERY (1986) and Anonymous, (1998). In the parts of Australia relevant to this paper (New South Wales, A.C.T. and Tasmania), radiata pine is grown on a strip of 400 kilometres from the coast (limited mainly by rainfall). Some key issues in growing this species are listed by MACLAREN (1993).

The major product categories in which New Zealand's radiata pine is exported are (listed according to decreasing dollar amounts) – logs and poles; sawn timber; newsprint; chemical pulp; fibreboard; various forms of paper and paperboard; mechanical pulp and plywood (Anonymous, 1998). Solid wood uses include building construction; interior fittings and fixtures; furniture and components; pallets, crates and boxes; fencing, marine and freshwater piles; and particleboard (Anonymous, 1996b). Radiata pine grown in Australia is mainly used to make pulp, paper and sawn timber (Anonymous, 1997b). The major use of sawn lumber in Australia is for house framing. Some feel (especially in New Zealand) that markets for radiata pine wood will not grow as fast as the supply. Given that neither New Zealand or Australia can grow conifer wood and deliver it cheaply to the world market, there is a clear need to use breeding to both reduce costs and improve quality.

The importance of this species has warranted active breeding programmes in both countries since 1950 (ELDRIDGE, 1983; BURDON, 1992a; BOOMSMA, 1997). Breeding was largely done by government organisations (Forest Research Institute in New Zealand, CSIRO and State Governments in Australia) up to the 1980s. As the New Zealand government reduced its role in forestry, particularly by disbanding the Forest Service and selling its plantations, industry began to play a bigger role in tree breeding. The New Zealand Radiata Pine Breeding Co-operative (NZRPBC) was formed in 1987, and now has 15 members – 11 New Zealand companies, three Australian companies (based in south-eastern Australia) and Forest Research. These organisations control over a million hectares of planted radiata pine.

The breeding programme is described in SHELBOURNE et al. (1986), Anonymous (1987), SHELBOURNE *et al.* (1989), CARSON *et al.* (1990), JAYAWICKRAMA *et al.* (1997a) and VINCENT (1997). The programme has had the stages common in conifer breeding programmes: plus-tree selection in unimproved plantations, ranking of GCA using open-pollinated progeny tests and the crossing of well-ranked parent clones to generate advanced-generation selections. Over 2,650 parents have been progeny tested, and over 1,500 control-pollinated crosses tested and screened for advanced-generation selections, involving first-, second- and third-generation clones. A large number of parent clones are available in archives, at least 1300 as of 1998. There are, however, two aspects of the New Zealand breeding programme less common in conifer breeding programmes. The first is the advancement of breeding populations for specific traits / product goals / site types, starting with a Long Internode breed in 1970. The second aspect has been the structuring of the breeding population into two superlines. These topics are discussed further under the section "Existing Breeding Strategy".

A detailed breeding plan for the New Zealand radiata pine breeding programme was documented by SHELBOURNE *et al.* (1986). Since then there has been a gradual evolution of the strategy, culminating in a revision in 1997 to 1999. The aim of this publication is to document the New Zealand radiata pine breeding strategy as of early 1999 with emphasis on developments subsequent to 1986. Three topics are presented: the previous breeding strategy, the process of revision and the revised strategy.

Previous Breeding Strategy

The current strategy of the New Zealand radiata pine breeding programme (up to and including the 1986 breeding plan) can be described under several topics:

Base Population

There are five natural populations of radiata pine, three on the Californian coast and two on islands off the coast of Mexico (LIBBY, 1997). The first definitely known introduction of *P. radiata* to New Zealand was from England in 1859; later importations of *P. radiata* seed and plants took place from the United States, England and Australia (SHEPHERD and COOK, 1988; SHEPHERD, 1990). It appears that the New Zealand land race stocks are almost entirely derived from the Año Nuevo and Monterey populations (BURDON *et al.,* 1997a). Similarly, there is evidence that the Australian land race stocks are derived from Monterey and Año Nuevo (MORAN and BELL, 1987).

The five provenances have been well tested in New Zealand and Australia (ELDRIDGE, 1997). In general the New Zealand land race stocks have outperformed the native provenances for growth, form and adaptation in New Zealand (BURDON *et al.,* 1997a), vindicating the early decision to base the breeding population on this land race (THULIN, 1957). The superiority of the land race over the native provenances has been attributed to natural and silvicultural selection (SHELBOURNE *et al.,* 1986) taking place over 100 years or so. In terms of advancing a native provenance as a population, the most interest in New Zealand has been in Guadalupe. Selections have been made in tests of open-pollinated families, and other plantings in New Zealand, from seed collected on the Guadalupe island. Useful attributes of this provenance include good wood density, stiffness, form and resistance to toppling; breeding is underway to make use of these features (LOW and SMITH, 1997).

Breeding Goals and Selection Criteria

Breeding Goals

The importance to a genetic improvement programme of having a breeding objective has been stressed by animal breeders (e.g. PONZONI and NEWMAN, 1989) and more recently in tree breeding as well (WOOLASTON and JARVIS, 1995). Reports on breeding objectives for conifer breeding programs are nevertheless rare. Breeding objectives have not been defined for the New Zealand radiata pine programme to the extent specified in some reports (e.g. PONZONI and NEWMAN, 1989; BORRALHO *et al.,* 1993). However the programme has what could be called 'breeding goals' or approximations to breeding objectives. In some cases they were instituted implicitly rather than explicitly. For example, THULIN (1957) refers to a "ideal tree type" yielding "highest quality timber" and having light multinodal branching, straight stem form, high heartwood content, above average growth rate and resistance to diseases.

The longest standing breeding goal has been producing large, fast-grown and well-formed logs; this came to be known as the "Growth and Form" breed. This could be said to date back to the inception of the programme in 1950. To that was added the goal of increasing the production of knot-free lumber from unpruned trees (1970; the "Long Internode" breed; see JAYAWICKRAMA *et al.,* 1997b), planting on sites highly conducive to Dothistroma needle blight (1983; the "Dothistroma-resistant" breed; see CARSON, 1989), and increasing wood density (1986; the "High Wood Density" breed). These breeding goals are shown in *table 1.*

Table 1. – Breeding goals and trait emphases for the different parts of the breeding population.

Breed	Goal: Improved Profitability of producing..	Special emphasis on
Growth and Form breed	large, well-formed logs	excellent growth and form
Structural Timber	strong, stiff, stable timber with small knots	high stiffness, highly multinodal, low spiral-grain angle
Clear Cuttings	clear wood from unpruned trees	moderate to long internodes, good appearance
Dothistroma-resistant	trees on sites with high Dothistroma pressure	good growth, low Dothistroma infection
Long Internode	knot-free wood from unpruned trees	long internodes, growth rate
High Wood Density	dense timber	wood density
Main Population	all the above, by serving as a long-term source of genetic variation	growth, form and crown health
Guadalupe	large, well-formed logs and strong, stiff, stable timber	growth, form, crown health, wood density and stiffness

Selection Traits

After early experimentation, six traits have been routinely assessed since 1983. They are stem diameter (dbh), straightness score, branch cluster frequency score, needle retention score, malformation score and acceptability for final crop. Ranking families for wood density started in 1975. A summary of the selection traits and the purpose for assessing them is given in *table 2.* Information on the inheritance of several of these traits is given by CARSON (1989), KING and BURDON (1991), BURDON (1992b), JAYAWICKRAMA *et al.* (1997b) and KING *et al.* (1998). In general, heritabilities are moderate to high; the highest heritabilities are typically for wood density while heritabilities for malformation and acceptability are low. A recent study of 95 wood- or end-product characters, made on 16- and 28-year-old clones, showed high broad-sense heritabilities for almost every trait studied (SHELBOURNE, 1997).

Population Structure

Superlines

The breeding population was divided into two superlines in 1988, keeping relatedness within superlines (BURDON, 1986). This was done so that crosses between superlines (in control-pollinated seed orchards for example) would be unrelated (CARSON *et al.,* 1990) and with control-pollinated orchards seen as the main means for future seed production (CARSON, 1986). Prior to this division the breeding population was essentially a single population plus a separate long internode population. Two-superline structures were later adopted in the slash pine and Southern Tree Breeding Association (STBA) radiata pine breeding strategies (WHITE *et al.,* 1993; BOOMSMA, 1997).

Non-Regionalised Breeding Programme

Since the 1980s there has been one breeding programme for the whole of New Zealand (CARSON *et al.,* 1990), as trials had shown that the extra gain from regionalised programmes would not be enough to warrant the extra cost (CARSON, 1990; JOHNSON and BURDON, 1990). Good genetic correlations have been obtained for growth and form between sites in New Zealand and in New South Wales, Tasmania and Victoria (JOHNSON *et al.,* 1988; BURDON *et al.,* 1997b). Some of the correlation estimates between New Zealand and Australian sites were higher than the estimates within New Zealand, or within Australia.

While not strictly a regional breed, the Dothistroma resistant breed is a response to a specific environment (i.e. areas with a high incidence of Dothistroma needle blight).

Main Population and Breeds

The breeding population was partitioned into a main population and several breeds, starting with the formation of a Dothistroma-resistant breed in 1983 (CARSON and CARSON,

Table 2. – Selection traits routinely assessed in the NZRPBC trials.

Trait	Units	Description	Goal in assessing trait: Improve.	Applies to which Breeding Goal	References
Diameter	Milli-metres	At 1.4 metres height, over bark	Log size	All	
Straightness	1 to 9 scale	1 = most crooked[1], 9 = very straight[1]	Log quality	All	
Branch Cluster Frequency	1 to 9 scale	1 = fewest clusters[1], 9 = most clusters[1]	i) Clearwood yield from unpruned stems and ii) reduce branch size	Long Internode, Clear Cuttings, Structural Timber	JAYAWICK-RAMA *et al.* 1997b
Malform-ation	1 to 9 scale	1 = many forks[1], 9 = no forks or ramicorns[1]	Log quality	All	
Acceptability	0 or 1	0 = judged not to give an acceptable crop tree, 1 = acceptable	Log quality	All	
Dothistroma infection	1 to 9 scale	1 = no infection, 9 = $\geq$ 90% infection	Log size, by reducing Dothistroma needle blight	Dothistroma Resistant breed	CARSON 1989
Needle Retention	1 to 6 scale	A year's full foliage = 2 points	Log size, by reducing *Cyclaneusma* needle cast	All	LOW 1991, KING and BURDON 1991
Density	Kg/m3	Assessed using water displacement, on 5mm cores	Stiffness, strength	High Wood Density, Structural Timber, Guadalupe	
Spiral Grain Angle	Angle from stem axis	Measure on two opposing sides of tree, at breast height using the bark window method	Stability of wood	Structural Timber, Clear Cuttings	SORENSSON *et al.* 1997

[1]) For the site

1986) and a High Wood Density breed in 1986. These breeds were partly disconnected from the main population. Discrete control-pollinated populations were subsequently established for these breeds. In addition to these populations, a Long Internode population was formed in 1970; this has been disconnected from the rest of the breeding population to date.

These populations correspond to the breeding goals listed previously. The option of forming breeds practised in New Zealand, while not seen precisely that way at the time, effectively combined the "elite population" and "multiple population" concepts (NAMKOONG, 1976; COTTERILL *et al.,* 1989; ERIKSSON *et al.,* 1993).

Selection Strategy

Emphasis on General Combining Ability

In common with other tree breeding programmes, the main approach has been recurrent selection for additive effects (general combining ability or GCA). This method has been discussed by several authors (e.g. SHELBOURNE, 1969; MCKEAND and BRIDGWATER, 1998). This strategy has been validated in the breeding population by large realised gains and by evidence that specific combining ability (SCA) for growth rate, while large at first, declines in importance with stand age when compared with GCA (CARSON, 1990; KING *et al.,* 1998).

GCA Testing and Recombination

Open-pollinated progenies from parent ortets and polycross progenies have been used to rank parents. Since the late 1980s the *female tester* method, namely a NC-II type design with five standard female testers, was used specifically for the estimation of GCA. This method eliminated bias caused by seed size and other maternal effects; although it increased the crossing workload, the total number of trees planted was kept to that for polycross testing.

GCA ranking and recombination for future selections were thereby separated (BURDON and SHELBOURNE, 1971; CARSON *et al.,* 1990). The female tester method has been used for first- and second-generation selections originating from New Zealand landrace stocks, selections from the Guadalupe provenance grown in New Zealand, and 30 Australian selections; 958 female-tester crosses have been made. Trials with the first 150 genotypes were planted in 1992 to 1993, with each full-sib family planted on three sites. A second smaller group was planted in 1997.

Testing and Selection Protocols

Progenies have been tested on an average of three sites, including one from the central North Island. A minimum of three trials on good screening sites are needed to get good GCA estimates. Good trial sites in the central North Island are particularly effective for the screening of genotypes (CARSON, 1990). A sets-in-replications trial design has been used since 1969 (JAYAWICKRAMA and LOW, 1999). Selections within seedling progeny tests have been made as early as four years and as late as ten years; the standard now is near age eight which was shown to be optimal (KING and BURDON, 1991). At this age radiata pine reaches 16 meters in height and 25 cm dbh on good sites in New Zealand; breast high increment cores will have six to seven rings from the pith. The form and branch habit of the most valuable part of the stem (the first two logs) is best seen at this age, and it is also a good age to assess needle retention. Dothistroma-resistance is an exception and can be assessed three years after planting; wood properties vary in the optimum age for selection.

Between 1975 and 1983, 264 forwards (advanced-generation) selections were made in open-pollinated progeny tests (JAYAWICKRAMA *et al.,* 1997a). The more recent groups of forwards selections have been within control-pollinated tests and family blocks. Two large control-pollinated populations were established in 1980. Full-sib selection blocks were used twice on a large scale, with 324 families planted in 1985, and 90 long internode families planted in 1990. In parallel to female tester testing for GCA, the 1986 breeding strategy put emphasis on generating control-pollinated families for selection of superior genotypes.

Multi-trait, multi-site selection indices (BURDON, 1979) were routinely used in selecting first-generation parents (e.g. SHELBOURNE and LOW, 1980). These indices have invariably included dbh and straightness; depending on the breeding goal, branch cluster frequency, needle retention, malformation, wood density have also been used in various combinations. With the need to combine information across several generations, Best Linear Prediction was adopted in 1993 and subsequently Best Linear Unbiased Prediction in 1998.

Rationale for Updating The Breeding Strategy

Since the last developments on the strategy (1986 to 1989), the following had occurred:

First, many new selections had come available, for recombination, to obtain genetic gain and / or broaden the genetic base. Over 1,000 first-generation parent clones (from the New Zealand land race stocks) had been progeny tested, and a further 474 clones selected from Australian land race stocks could be added. One hundred and twenty eight selections were made in 1994 within New Zealand plantings of the native provenances. An efficient, well-considered strategy was therefore needed for recombination.

Second, there had been changes in emphases and practices in plantation forestry. Rotation lengths had dropped, below 25 years in some cases in New Zealand. This led to a greater awareness of the effects of juvenile wood on wood quality. The commercial deployment of control-pollinated seed as seedlings or cuttings, and full-sib blocks, had both increased.

Third, new members had joined the NZRPBC after the previous strategy was formulated, including three Australian organisations. The co-operative's strategy had to accommodate their needs and priorities (site types, production objectives etc.) as well.

Fourth, major overseas conifer breeding programmes such as the Southern Tree Breeding Association, the North Carolina State University- and University of Florida- based co-operatives and CAMCORE had updated or formulated their breeding strategies (WHITE *et al.,* 1993; Anonymous, 1996a; BOOMSMA, 1997; MCKEAND and BRIDGATER, 1998). There was therefore an opportunity to draw on their advances and developments.

Summarising these developments, we could say that the genetic base has broadened, new breeding goals and selection criteria have come to the fore, and breeding concepts and technologies have changed.

Revision of the Breeding Strategy

New Breeding Goals and Selection Traits

While updating the strategy, two new breeding goals were accepted. They were the increased profitability of producing (i) strong, stable timber, and (ii) clear wood from unpruned trees (the "Structural Timber" and "Clear Cuttings" breeds respectively). Routine assessment of spiral grain angle started around 1995. A direct or indirect method for assessing stiffness will shortly be selected, followed by methods to assess appearance. Other wood traits and new pests or pathogens could well become important in the future. The breeding goals and traits emphasised for the two new populations are shown in *table 1,* and details on the assessment of spiral grain angle in *table 2.*

Relative Trait Emphases

The formulation of economic weights is a continuing research goal. One approach taken by the New Zealand radiata pine breeding programme is the use of simulation models integrating data on sites, growth rate, silviculture, harvesting and processing (CARSON, 1988; WITEHIRA, 1996). Members of the co-operative place different emphases on different traits based on their product requirements. For this revision, traits were ranked in the following order (highest first):

• growth rate and stem straightness, wood density, spiral-grain angle, distance between branch clusters, microfibril angle, wood stiffness, proportion of compression wood, Cyclaneusma-resistance, Dothistroma-resistance.

Simulation of Main Population and Breeds

Before changing the breeding strategy, potential genetic gains were tested for alternate options. This was done using a programme by which the simultaneous advancement of multiple traits (e.g. Dbh, straightness etc.) could be simulated stochastically (JAYAWICKRAMA and JEFFERSON, 1999). A "large" main population was compared with four 'breeds' with emphasis on different traits: a "Structural Timber" breed (multinodal habit, high wood density and low spiral grain angle), a "Growth and Form" breed (dbh and straightness), a "Clear Cuttings" breed (moderate- to long internodes and low spiral grain angle) and a "Fibre" breed (dbh and high wood density). The results showed that each hypothetical breed would get more gain (in one or more traits) than the main population, mostly due to the higher selection intensity exercised on the parent clones (JAYAWICKRAMA and JEFFERSON, 1999). In no case did the breeding result in undesirable change of any trait compared with the base population.

Revised NZRPBC Strategy

The breeding strategy recently adopted by the NZRPBC is now outlined.

Key Features of the Revised Strategy

The strategy will keep the following aspects of the existing strategy used in breeding radiata pine in New Zealand: a two-superline structure; emphasis on recurrent selection for GCA; a non-regionalised breeding programme; and a final selection at around age eight years in control-pollinated populations. It will also give priority to the breeds compared to the main and Guadalupe populations; give high priority to improving corewood quality, in addition to improving growth rate, form and adaptability; and only use GCA-tested parent clones in the breeds (for the current cycle of testing). Most of the parents included in the main population will also be GCA-tested.

Two new breeds are to be formed, a third breed and the Main Population are to be expanded, and the Guadalupe breeding population is to be integrated into the breeding population. The breeds will be tested as full-sib families, either as seedlings or as clones within families. The main population and the Guadalupe breeding population will be tested as seedlings. The status number of the parent clones involved in the breeds, main and Guadalupe population (during this cycle) is about 400.

Breeds

Two new breeds (Clear Cuttings and Structural Timber) will be developed while progressing two existing breeds (Growth and Form, Dothistroma resistant). The breeds will be small populations of highly-ranked genotypes selected for different breeding goals. Threshold values for growth rate, stem form, Dothistroma resistance, Cyclaneusma resistance, stiffness and spiral-grain angle will be maintained in all the breeds; the thresholds may differ for different breeds. The traits to be emphasised in each breed are shown in *table 1.* Reasons for continuing the strategy of differentiating breeds are discussed in JAYAWICKRAMA *et al.,* (1997a), and include: 1) the high phenotypic plasticity of radiata pine and its potential for a variety of uses 2) greater genetic gain (at least for the first couple of generations) in specific traits and 3) a clear focus on end-product quality. The gains in 'internode' length obtained in the Long Internode breed (JAYAWICKRAMA *et al.,* 1997b) were a striking example of what could be achieved by intense selection on a targeted trait.

The breeds will fit in to the existing superlines of the NZR-PBC. In terms of numbers of parents and crosses, the goal is a minimum of 24 parents per breed (12 in each superline) and 36 crosses per breed (18 per superline). This translates to each parent crossed three times, in disconnected 6-parent factorials. Disconnected factorials are an efficient mating design for selecting within progenies (VAN BUIJTENEN and BURDON, 1990); these authors also found that the relative efficiency with 3 crosses per parent was 96% that of 25 crosses per parent.

The Structural Timber breed was partly motivated by the importance (to Australian growers) of structural timber, and the suitability of Australian sites and silviculture for this product. The new Clear Cuttings breed continues the goal of growing knot-free wood seen in the Long Internode breed; however there will be emphasis on grain spirality and wood appearance, more emphasis on form, and less emphasis on very long "internodes". The goal for this breed is a healthy tree with good growth rate and straightness, free of malformation, low grain spirality and a high proportion of internodes exceeding 80 cm in the first two logs.

A Growth and Form breed was established in 1992 to 1993, and will be expanded by crosses between new progeny-tested, first-generation selections. The *Dothistroma*-resistant breed has already been formed with 52 parents and trials have been established. Two other populations, namely the Long Internode and High Wood Density populations, were established in 1990 and 1995 respectively. Parents and forwards selections from these populations can be fed into seed orchards and the four breeds. The relationship between the existing and future breeds is shown in *figure 2.* The options of developing "Appearance-Grade Timber", "Fertile / Farm Site" and "Fibre" breeds

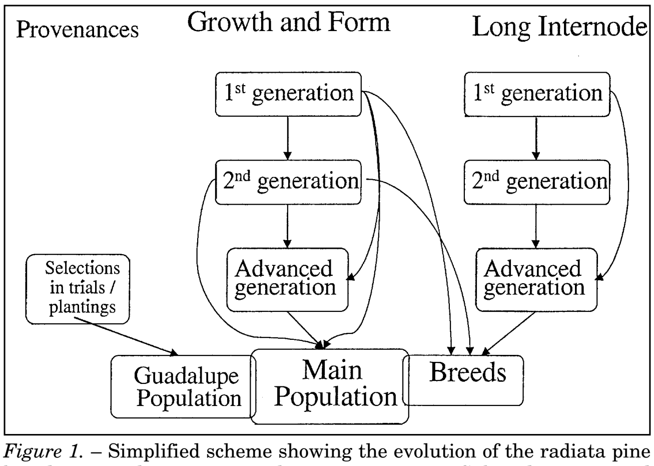

Figure 1. – Simplified scheme showing the evolution of the radiata pine breeding population, up to the current NZRPBC breeds, main and Guadalupe populations.

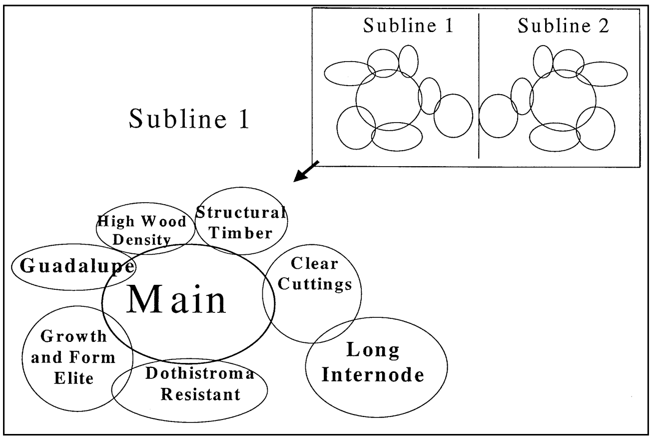

Figure 2. – Relationships and overlap between current components of the NZRPBC breeding population.

were considered (JAYAWICKRAMA *et al.,* 1997a), but eventually dropped.

Main Population

The main population will maintain long-term variability and effective population size ("Genetic Insurance"), and to feed new candidates into breeds and the production population. Given the number of selections present (many of them progeny-tested), there will be many that grow well, and are well-adapted but are not immediately suited for the current breeds (clear cuttings, *Dothistroma*-resistant etc.). The focus of the breeding population is rather a general improvement of forest-growing and wood-quality traits.

A main population was established in 1992 to 1993, in which 125 parents (first-, second- and third-generation) were crossed. A second phase of control-pollinated breeding and testing is now planned, adding a further 100 parents and bringing the total to 225. These 100 new parents will be drawn from those recently made available, including first-generation progeny-tested parents from New Zealand and from New South Wales and advanced-generation selections. These parents are to be crossed together generating 100 crosses, as pair-crosses or in a double-pair mating design. The objective is to select 225 new breeding-population clones at the end of the cycle, from the 225 crosses generated in the two phases.

Guadelupe Breeding Population

Sixty-seven parents have been selected, within open-pollinated progeny tests and other plantings of this provenance in New Zealand, to form a breeding population. They are being crossed together to generate about 70 full-sib crosses, in a way that promotes outcrossing: using the location of the mother trees on Guadalupe island, the goal is to make at least one cross (per selection) with another selection whose mother tree was located at least 1 kilometre distant (LOW and SMITH, 1997). The crossing programme will be completed by 1999. The best of the Guadalupe parent clones will also be introgressed with the land race selections in order to recombine alleles unique to, or at higher frequency in, this provenance. The Guadelupe population will also fit as two sub-populations within the two superlines.

Testing Procedures

The mechanism for testing candidates within the breeds will be one of the following two options. The first option is to clone 10 to 20 seedlings per full-sib family, and test them as ramets (nominally six ramets on each of four sites). This would result in 240 or more trees planted per cross. The second option is to test the full-sib families within a breed as seedlings, also on four locations chosen to differentiate the families for their breed characteristics. Under this second option there would be a total of about 120 trees planted per family. The final choice will depend on evaluating the benefits and costs for each, and may differ for each breed.

Future locations for testing the breeds will include high-fertility sites and *Dothistroma*-susceptible sites, and other suitable sites in both New Zealand and Australia. Data from specific site types will allow for selection of a subset of both orchard parents and production clones matched to site and production goals. A strong emphasis will be given to testing the Structural Timber breed in Australia, where the objective of this breed is a high priority.

Both the main and Guadalupe populations will be tested only as seedlings. The full-sib families will be tested at four locations, with a total of about 120 trees planted per family. Apart from those clones that have already been ranked in open-pollinated trials or crossed with the female testers, no further GCA testing of these populations is envisaged in the current cycle of breeding. Trial designs to be used in this cycle of testing are under review.

Links Between the Main Population, Breeds and the Production Population

The production population can be formed from whatever elements of the breeding population are appropriate. In many cases production crosses will be made between parent clones within a breed. In other cases, the most appropriate crosses may be between breeds, resulting in progeny intermediate between the breeds. It is quite feasible now to make unrelated production crosses within superlines, but this will become harder in future generations as inbreeding builds up within superlines.

The breeds, main population and the Guadalupe population will be linked by common crosses and control seedlots in order to facilitate between-breed comparisons of breeding values. The best selections from the main population or the Guadalupe breeding population will be fed into breeds, giving extra genetic gain and slowing the build-up of inbreeding. There is no plan for gene flow in the opposite direction. The number of parents in the production population will always be less than in the full breeding population.

Population Size, Mating Designs and Inbreeding

The number of parent clones in the breeds, main population and the Guadalupe population are given in *table 3.* There has been overlap between populations in the selection of parent clones; overlap will be kept to a minimum in the new populations being formed. The concept of "Status Effective Number" or "Status Number" is a measure of the genetic diversity of breeding populations (LINDGREN *et al.,* 1996). The status number (Ne) can be interpreted as the size (or census number) of a population free of inbreeding and comprised of unrelated genotypes. The total number of parents involved in the current breeding strategy (= census number) and the status number were calculated, pooling information across the breeds and main population. The resulting numbers, at 545 and 400 respectively (both less than the sum across populations, owing to overlap), are adequate given the radiata pine plantation estate in New Zealand and Australia (about 2.2 million ha).

These numbers can be compared with reports for two breeding programmes in the south-eastern United States: 160 mainline population selections, per geographic region, for the third-cycle loblolly pine (*Pinus taeda* L.) programme described

Table 3. – Control-pollinated populations established or planned by the NZRPBC for advanced generation selection.

Breed	Number of parent clones	Status Number	Number of crosses	Area of trials	Trials planted in / to be planted in
EXISTING					
Growth and Form breed (1)	26	22.1	49	14.7	1993, 1999[1]
Dothistroma-resistant	52	49.6	46	12.1	1994, 1995[1]
Long Internode	128	99.6	133	23.8	1990
High Wood Density	45	42.6	20	5.8	1995
Main population (1)	146	92.9	120	14.5	1993
PLANNED					
Growth and Form breed (2)	14	14.0	18	7.4	2005
Structural Timber	24	23.2	36	14.8	2003
Clear Cuttings	24	23.0	36	14.8	2004
Main population (2)	100	90	100	21.2	2002
Guadalupe population	67	56.5	70	16.2	2000

[1]) A subset of the families, as clones

by McKeand and Bridgwater (1998); and a breeding population of 933 trees (effective population size of 625) for the advanced-generation slash pine (*Pinus elliottii* Engelm. var *elliottii*) programme (White *et al.*, 1993). The latter programme is for an estate of 4 million hectares of slash pine.

From the numbers given above for the NZRPBC radiata pine population (across multiple breeds and populations), a viable breeding population can be maintained for a long time. With prudent management, inbreeding need not build up to critical levels even within the breeds for several generations. For example with a population size of only 12, a double-pair mating design and selecting one individual per full-sib cross, the nominal inbreeding coefficient (F) can be kept below 0.1 at the end of four generations of crossing and testing (GEA, 1997). Methods to slow inbreeding include keeping the number of parents high, keeping the number of crosses per parent low and making forwards selections in more families (assuming fixed resources).

There can be, however, a trade-off between short-term genetic gain and build-up of inbreeding. For example, the use of disconnected six-parent diallels as the mating design, with 2.5 crosses per parent clone, gives greater short-term gain but tends to speed up inbreeding (GEA, 1997). The current breeding strategy has a parent crossed three times on average in the breeds and twice in the main population. Emphasis is given to breeds compared to the main population not so much by making more crosses per parent, than by more investment in assessing their wood properties and the likely use of cloning.

The present mating design for the breeds (small factorials) has the advantage that parents can be dropped if found deficient for important traits. The approach has been to select parent clones on the best information available, start crossing and cull parents before the trials are planted (rather than delay the crossing). More parents were selected than the target number. For example parent clones in the Structural Timber breed met criteria for growth rate, straightness, branch habit, spiral grain-angle and juvenile wood density. Crossing is to be completed by 1999, and trials are planned for the year 2003. The mating design allows us to cull up to a third of the parent clones if they prove (based on assessments completed before trial establishment) to be sub-standard for stiffness and stability.

Workload

The number of crosses and area of trials (to date and planned) is given in *table 3*. The respective totals are of 371 crosses made and 70.9 ha. of trials planted for the period 1988 to 1996, and 290 crosses and 79.4 ha. planned for 1997 to 2005. In the previous period (1975 to 1986), 670 crosses had been made and 117.6 ha trials planted for advanced-generation selections.

Release of New Improved Genotypes

Discrete pulses of forwards selections will be provided by this strategy. These will probably be selected using Best Linear Unbiased Prediction methodology, incorporating parental information in addition to the trial results. The dates for release of new genotypes can be calculated by adding 8 to 12 years to the dates of planting given in *table 3.* The earliest group will be of long internode clones in 1999 to 2000, and the latest will be from the second part of the Growth and Form breed (after the year 2013). Major breakthroughs in early selection could reduce the time lag to obtaining these improved genotypes. Upon selection, there is usually a delay of several years before the new clones can make a major contribution to reforestation. Reducing this delay is an important goal of deployment research.

Future Composition of the Breeding Population

The target breeding population upon completion of the current cycle will have about 375 individuals; 225 selections from the two phases of the Main Population, 100 from the four breeds (GF Elite, Clear Cuttings, Structural Timber, Dothistroma resistant), and 50 from Guadalupe. The target status number will be 300 or greater. These 375 individuals will probably still include outstanding first-generation parents in addition to parents from later generations.

Gene Resource Population

A large investment has been made in seed collection, trials and conservation plantings of the five native provenances in New Zealand (Burdon *et al.*, 1997; Eldrige, 1997). This is in addition to a very large number of tested parent clones in archives, originating from the land race. This resource of native population selections and tested parent clones needs to be managed to underpin the breeding programme. Likely measures for the native population selections are: collect open-pollinated seed before the existing conservation plantings are felled, store this seed and plant new stands before seed viability declines; keep (in clonal archives) the selections made to date; and introgress the best Año Nuevo, Monterey, Cambria and Cedros selections into the main population. The other tested parent clones are likely to be kept in archives for the foreseeable future, particularly for the contingency of changed trait emphases.

Deployment of Improved Genetic Material

The first production of seed from open-pollinated orchards was in 1966, but it was not until 1985 that orchard seed met the New Zealand planting need (VINCENT, 1997). From that point onwards little unimproved seed was used for reforestation in New Zealand. About 50% of the planting in New Zealand is by farm foresters, investment companies and small companies outside the NZRPBC; they can nonetheless buy genetically improved seed and planting stock. Increasingly seed from control-pollinated seed is being used, deployed on at least 25% of the current planting. One company is planting clones on an operational scale. Genetically improved, open-pollinated seed from New Zealand, has been sold in Australia since 1988; more recently control-pollinated seed has been sold as well.

The genetic composition of the radiata pine production-population is dynamic. As data comes in from trials with new progenies and/or new traits, breeding values are updated and the choice of production parents can change rapidly. Most recently this occurred with the ranking of top production parents for wood spiral grain angle. A major driver of these changes is the improved public perception of genetic gains arising from the certification of genetic quality of seed.

The Seed Certification scheme started in 1987, and was based on growth and form data (Anonymous, 1987). All radiata pine seedlots sold were classified by a seedlot number made up of four components: the Breed Code, Improvement Rating, Year of Collection and Collection Number (VINCENT, 1987). This scheme was widely accepted, to the point of strongly influencing the market price of seed and plants; seed with the highest Growth and Form rating have on occasion been sold for 8.000 NZ $ per kilogram. The single improvement rating is now being replaced by the GF Plus™ system, which gives individual trait ratings for six traits to buyers of seed and plants (Anonymous, 1997c; VINCENT and BUCK, 1998). The six traits are growth, straightness, branch cluster frequency, resistance to *Dothistroma,* wood density and spiral grain angle. The ratings are based on breeding values calculated using mixed model methodology. GF Plus™ is likely to be expanded to include the Juvenile Wood Quality Index (JWI), which is being developed to rank production parents on the predicted quality of juvenile wood (Anonymous, 1997c).

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Genetic Analysis of Isozyme Variants in Open Pollinated Families of Southern Beech *Nothofagus nervosa* (PHIL.) DIM. et MIL.

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Abstract

Nothofagus nervosa (= N. alpina) represents one of the most important native tree species among the Southern Southamerican Temperate Forest. Its ecological situation in Argentina with a very reduce distribution area, overexploitation in the past, recurrent forest fires and overgrazing makes it a suitable species for conservation and improvement programs.

In order to conduct a complete population genetic study of the species in Argentina, isozyme gene markers were determined. Genetic analysis of the observed phenotypic variation was done applying the method described by GILLET and HATTEMER (1989). Twelve loci were analysed corresponding to six enzyme systems. Four of them were monomorphic, but two had species-specific alleles. Among the remainder, genetic control could be demonstrated in five loci and hypothesis on the mode of

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