Achievements in forest tree improvement in Australia and New Zealand 8. Successful introduction and breeding of radiata pine in Australia

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Summary

Radiata pine (*Pinus radiata*) was originally known as *Pinus insignis* or 'remarkable pine', an apt name for a tree which has had such a dramatic impact on the world timber scene. It is a native conifer of California, USA, and was first introduced into Australia around 1857 for ornamental plantings. There were two major sources of original importation, one through Ferdinand von Mueller to Victoria and South Australia in the 1860s, and the second through New Zealand seed merchants. Forty-year-old trees were clearfelled for sawing in 1908 in Victoria. The fast early growth of radiata pine in Mount Gambier and north of Adelaide in the 1870s and 80s prompted the state forest services of South Australia, Victoria and New South Wales to advocate planting of the remarkable pine as an exotic conifer to compensate for the relative paucity of indigenous softwood in Australia.

There was some plantation development in the 1920s and 1930s, but planting almost stopped during World War II. Large-scale planting of radiata pine started again only in the late 1950s. Up to the late 1960s, unimproved seeds used to establish plantations in Australia were at first from early ornamental plantings, then from small plantations and later, in part, imported from New Zealand. Initial research and breeding were undertaken by the Forestry and Timber Bureau (at Canberra and Mt Gambier) and the Queensland Forestry Department — both studied reproductive biology, selected superior trees and established progeny tests in the early 1950s. Following the Seventh British Commonwealth Forestry Conference in Australia and New Zealand in 1957, the other five state forest services and two private companies initiated genetic improvement work in the late 1950s. After establishment of the first grafted seed orchard in 1957, a total of 145 ha of seed orchard was established by 1968. Large-scale plantings using improved seeds started in the early 1970s. Many clones were received from NZ before the 1970s, and a range-wide seed collection was made in the five native stands in California in 1978.

In 1983, the Southern Tree Breeding Association (STBA) was formed to coordinate the national breeding program of radiata pine, and it now serves about half of Australia's radiata pine estate. The other half is controlled by Forests New South Wales (FNSW) and the Western Australian Forest Products Commission (FPC). Radiata pine has been bred for three generations since the 1950s, with realised genetic gain up to 33% for volume from the first generation and more than 10% gain predicted from the second generation. The focus of the third-generation breeding in STBA has shifted to wood quality traits with:

- integration of quantitative genetics, molecular genetics and wood science
- development of economic breeding objectives
- application of best linear unbiased prediction (BLUP) and a Web-based interactive database for customised delivery of breeding values.

During 50 years of breeding radiata pine in southern Australia, several changes in strategic directions have been developed and implemented. Options for such flexibility must be maintained. To further increase genetic gain, infusion of new genetic material from the range-wide collections, increased recombination rate and selection intensity, purging of inbreeding depression, deployment by clonal forestry, and development of strategies dealing with adverse genetic correlation between wood volume and quality traits will be critical.

Keywords: history; breeding programs; genetic improvement; genetic resources; provenance; traits; economics; wood properties; growth rate; information systems; radiata pine

Introduction

In 2006, the area of Australian softwood plantation was one million hectares (BRS 2006) — a significant milestone for the softwood industries. This was 130 y after Australia's first commercial pine plantation was established in 1876 at Bundaleer, South Australia (SA). Among the one million hectares of softwood, *Pinus radiata* is the predominant species (73% of softwood plantation) and is grown in all states and territories except the Northern Territory. *Pinus radiata* D.Don is referred to as *P. insignis* Douglas in older publications. Its common names in English are Monterey pine and radiata pine. In Spanish it is called 'Pino insigne' which means remarkable pine. It is indeed remarkable because of its fast early growth, wide adaptability and the distinctive shade of green of its foliage.

The purpose of this paper is to describe the history and genetic base of the radiata pine introduced into south-eastern Australia from California since 1857 and the continuing successful breeding programs for this species in an expanding plantation industry. It concentrates primarily on the successful program of the Southern Tree Breeding Association (STBA), which was formed in 1983, because it is arguably the most advanced, but notes significant progress made by other organisations in Australia, especially those in Western Australia (WA) and New South Wales (NSW).

Native radiata pine in north America

In contrast to the worldwide plantation area of radiata pine (about 4 million ha), there are only five small native populations with a total about 5300 ha in its natural habitats (Burdon 2001; Rogers 2002). The five populations occur between latitudes 28°N and 37°N; three are on the coast of California and two on islands off the west coast of Mexico (Fig. 1). Ecological habitats (soil, elevation, temperature, rainfall) differ substantially among the five populations, even though they share a regional Mediterranean-type, winter-rainfall climate. A cold ocean current to windward produces fog among the trees on most days during the almost rainless summer (Libby 1997).

The Monterey population is the largest natural radiata population and has about 3800 ha with estimated historical distribution about 7900 ha (Table 1). The second-largest is at Cambria, about 130 km south of Monterey, and has about 900 ha left with an historical size about 1400 ha. The smallest population on the mainland, at Point Año Nuevo, has about 450 ha. The southernmost population, Cedros Island, was estimated at about 150 ha, growing only on the ridgetops and upper windward slopes between altitudes of about 380 and 640 m. The Guadalupe Island population is nearly extinct, with only 220 trees distributed over an 8 km length of ridgetop up to 1200 m in altitude (Rogers 2002). The two island populations are sufficiently different to be considered taxonomic varieties (Burdon 2001).

Radiata pine importation to Australia

Foresters in the early twentieth century well recognised the potential value of exotic conifers in Australia, a country with so few indigenous softwood species and many relatively unproductive hardwoods. After a long process of species importation and trials, radiata pine from California was found to be the most productive and profitable species in the south-eastern states of Australia. However, early importation of radiata pine was for ornamental purposes and for restoration of gold mining sites, not for plantations per se. Various botanical gardens were involved in the early introductions. The earliest records show radiata pine was introduced at least as early as 1857, when the Sydney Botanic Gardens obtained one plant of radiata pine from Britain from the ship Duncan Dunbar (Fielding 1957). Ferdinand von Mueller, Director of the Melbourne Botanic Gardens, mentioned in a report dated 1858 that radiata pine was growing in the gardens (Grant 1989). Mueller was also responsible for distributing seven thousand radiata pine seedlings to Victoria and SA between 1861 and 1866 for ornamental plantings in gardens and for windbreaks on farms. In the Adelaide Botanic Gardens, radiata pine 15 m high (about 12 y old) was reported in 1878 (Lewis 1975). James Hector, Director of the Wellington Botanic Garden, imported radiata pine seed from California and distributed at least 25 kg throughout New Zealand between 1870 and 1879 (Shepherd and Cook 1988). The largest consignment, 11 kg in 1876, probably came from a large number of trees, perhaps more than 100 if

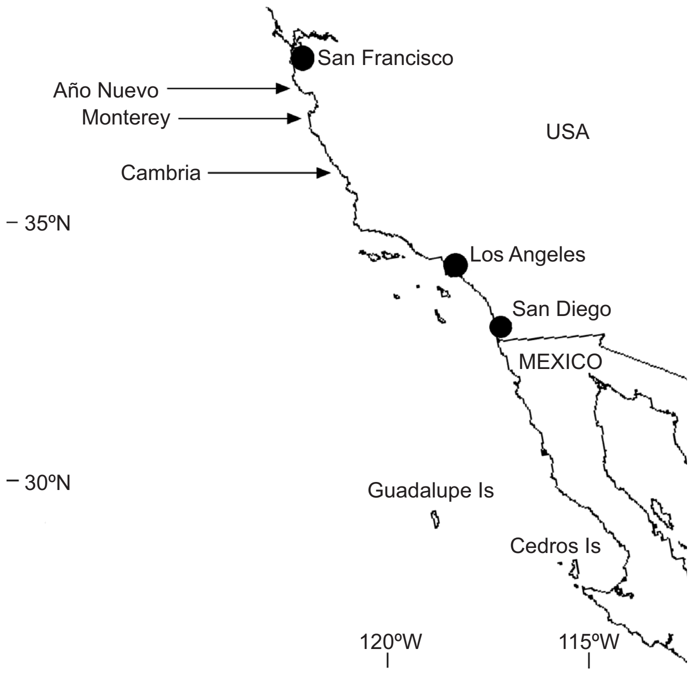

Figure 1. Natural distribution of radiata pine: West coast of north America and two island provenances on the Mexican islands of Guadalupe and Cedros

Table 1. Characteristics of the five native radiata pine populations (Eldridge 1978 and Burdon 2001)

Population	Latitude (°N)	Altitude (m)	Rainfall approx. (mm)	Area (ha)	Soil
Año Nuevo	37	10–330	800	450	Fine loams, depth variable
Monterey	36.5	10–440	400	3800	Very varied fertility and base status
Cambria	35.5	10–200	500	900	Sandy loam, localised poor drainage
Guadalupe Island	29	400–1200	300?	220 trees	Rocky loam
Cedros Island	28	380–640	200?	150	Skeletal

collection was at the rate of 40 cones per tree, about 100 g of seed per tree, as it was in the 1978 collection (Eldridge 1978).

Thus the early ornamental and windbreak plantings are almost certainly from a large number of parent trees in California, evidenced by surviving records of a large number of small consignments of seed and a few live plants between 1857 and 1879 (Shepherd and Cook 1988; Shepherd 1990). After about 1880 the early ornamental and windbreak plantings were producing abundant seed and there was no demand for further expensive importations. There has been no further infusion of wild genes into the plantation land races since about 1880.

The genetic base of the present Australian and New Zealand plantations has been shown to be from only Año Nuevo and Monterey, the two best-adapted of the five natural populations (Moran and Bell 1987; Burdon 1992).

Up to the late 1960s, the unimproved seeds used to establish plantations in Australia were at first from early ornamental plantings and windbreaks, then from small plantations and later, in part, imported from New Zealand plantations. During the 1960s, much of the radiata pine seed used in new plantations was still obtained from trees felled at harvesting or thinnings. It is likely that genetic bottlenecks and founder effects occurred after importation, because large seed collections were made in New Zealand and Australia from ornamental plantings and small plantations that were probably derived from few trees.

Considerably more genetic variation exists within unsampled parts of Año Nuevo and Monterey and in the three unused populations, Cambria, Guadalupe and Cedros. This material is available, if needed, in ex situ conservation plantings resulting from the 1978 range-wide seed collection (Eldridge 1997). The limited genetic base, described earlier, was nevertheless sufficient to provide the genetic variation successfully utilised for the economically significant genetic gain achieved in 50 y of breeding.

Radiata pine breeding in Australia

Preliminary work to assess genetic variation in radiata pine, using rooted cuttings, commenced in Canberra in 1937 and in SA in 1938 (Fielding 1970); it provided clear evidence of the significant role of genetic factors in the form and growth of this species.

The Forestry and Timber Bureau (at Canberra and Mt Gambier) and the Queensland Forest Department undertook follow-up research and breeding; both studied reproductive biology, selected phenotypically-superior trees (plus trees) and then established progeny tests in the early 1950s. Following the Seventh British Commonwealth Forestry Conference in Australia and New Zealand in 1957, the other five state forest services and two private companies initiated genetic improvement work in the early 1960s. The tree breeding work on radiata pine in the 1950s and 1960s followed very much conventional conifer breeding methods: selection and grafting of plus trees and establishment of clonal seed orchards with concurrent progeny testing. The first clonal seed orchard of radiata pine was established in 1957, 100 years after the earliest recorded radiata pine importation. A total of 145 ha of seed orchards were established by 1968 and 350 ha by 1976 (Shepherd 1977). By the late 1970s, more than 300 progeny trials had been established across NSW, the Australia Capital Territory (ACT), Victoria, SA, Tasmania, Queensland and WA. By 1970, the South Australian and Queensland forest services were the first radiata pine forestry organisations to use genetically improved radiata planting stock exclusively. By 1985, seed orchard seed was used for planting most Australian radiata pine plantations.

In the 1970s and early 1980s, radiata pine breeding was mainly carried out in separate programs of the six state forest services and private companies, with direct or indirect involvement of CSIRO (Eldridge 1983). Research Working Group One (RWG1 Forest Genetics) of the Australian Forestry Council played a significant role in fostering material exchange and information sharing between breeding programs. Recognising the importance of a coordinated program for advanced-generation breeding, CSIRO in the late 1970s initiated an Australia-wide diallel mating and testing program. In 1982, the STBA (an incorporated non-profit breeding organisation funded by industry organisations in the 'Green Triangle' region of south-eastern SA and western Victoria) was established with the assistance of CSIRO to conduct a radiata pine breeding program for two radiata pine companies and the state government of SA; it eventually expanded into a national breeding organisation. The Western Australian Forests Department (now the WA Forest Products Commission — FPC) was the first 'non-green triangle' organisation to join STBA (in 1989), but withdrew in 2000. Forests NSW (formerly the Forestry Commission of NSW) is not a member of STBA, but joined instead the New Zealand-based Radiata Pine Breeding Consortium.

During the 1980s, Forests NSW conducted a search of their post-World War II plantations and augmented their genetic base of 103 trees by 310 selections chosen at an intensity of about 1 : 6000). These were grafted into clone banks and tested in field trials. About 40 further selections were made in collaborative trials with CSIRO at about this time. New seed orchards were established at Tallaganda (with selections resistant to *Dothistroma*), at Windemere near Mudgee (from second-generation selections) and at Walcha. A seed orchard was also established more recently at Boydtown on the south coast of NSW. Progeny tests from these seed orchards aimed at testing selections and investigating genotype × environment interaction were established on many sites in 1992 (using 89 second-generation seedlots) and 1993 (with 42 second-generation seedlots). Principal breeding and deployment activities in NSW have been via the Radiata Pine Breeding Cooperative (RPBC — later 'Company' and now 'Consortium') and will be described in another paper[1].

The first major step in the STBA's breeding activities was the selection and progeny testing of 600 new radiata pine plus trees in the early 1980s (the Super-80 series) from plantations in the

[1]An account of radiata pine improvement in New Zealand, in preparation for this journal

Green Triangle (Boomsma 1997). In 1984, a plan for breeding radiata pine with two-stage selection was documented and published (Cotterill 1984). In 1987, a Nucleus Breeding strategy was proposed and adopted (Cotterill *et al*. 1989). In 1991–1992, the Nucleus Breeding strategy was thoroughly reviewed and significant modifications were made for the second generation of breeding (White *et al*. 1999). On the basis of this strategy, breeding values were predicted for 1213 first-generation parents and 1152 second-generation selections from 106 tests with about 300 000 trees. Consequent crossing work was carried out in the early 1990s. This led to the establishment of a large number (30) of control-pollinated progeny trials in 1996 and 1997 which now form the basis for much of the advanced-generation breeding effort on radiata pine in Australia. The essential elements of the second-generation breeding strategy developed and eventually adopted by STBA members in 1993 were:

- Nucleus and Main breeding populations (open nucleus of 40 selections, main of 300 selections)
- two unrelated sub-lines each consisting of three trait-based subpopulations (Multi-Purpose, Density and Growth, Growth and *Phytophthora* Resistance)
- two-way transfer between the Nucleus and the Main
- crossing for deployment between unrelated sub-lines.

During the 1990s, the system of deployment of radiata pine among STBA members changed from open-pollinated seed orchards to control-pollinated seed orchards, together with mass vegetative propagation by rooted cuttings. Recently, radiata pine breeding has advanced into a third-generation selection and mating scheme with planned multiple deployment populations. STBA membership has broadened to include organisations from other Australian states and New Zealand. Currently the STBA has ten breeding members and four research members active in the radiata pine breeding program. Figure 2 depicts the progress of breeding and deployment populations and method of breeding value prediction in the STBA radiata pine breeding history.

Radiata pine is the most important conifer species in WA although *Pinus pinaster* has overtaken radiata pine in recent plantation expansion (the areas of plantations of the two species are about 60 000 ha and 44 000 ha, respectively — BRS 2006). There are significant genetic resources of radiata pine in WA

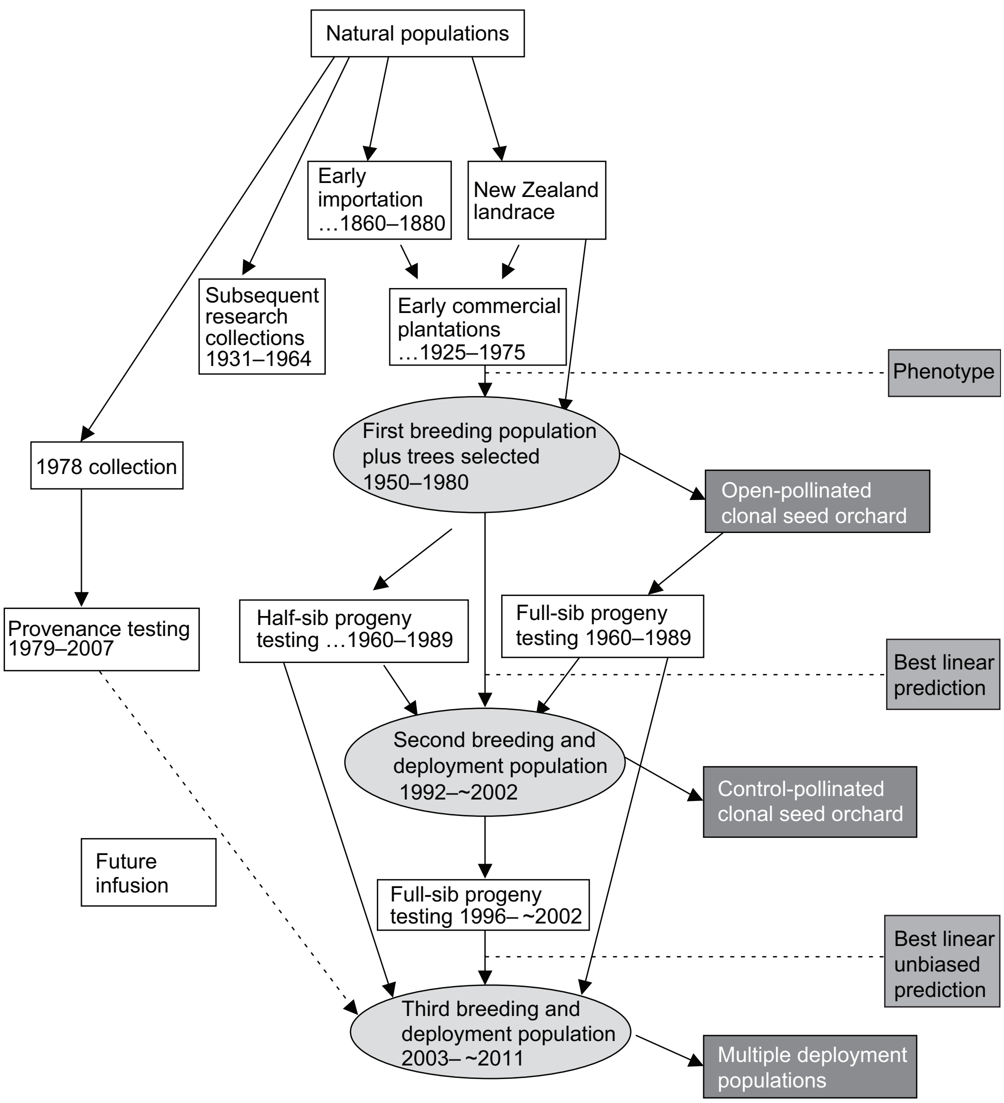

Figure 2. The generalised flow chart of radiata pine improvement in Australia

aimed at sites in the south-west of the state, away from the infertile sandy soils of the region around Perth. In addition to its STBA activities until 2000, the WA FPC made nearly 700 low-intensity selections from its own plantations in 1985 (the Search85 selections). These parallel similar selections in NSW and the Super80s in STBA. WA FPC is making use of selections from South Africa as well as STBA material and its Search85 selections. Trials derived from Cambria provenance material collected from the native stands in 1978 were also established[2]. This provenance will be useful because it has greater tolerance to *Phytophthora cinnamomi*, soil salinity, phosphate-deficient soils, waterlogging and marginal and dry conditions. WA has particular problems with *P. cinnamomi* and so selection for resistance has been of major importance in the FPC program (Butcher *et al.* 1984). Success has been demonstrated on a *P. cinnamomi*-susceptible site where a population bred for resistance had a basal area of 61 m^2 ha^{-1} compared with 37 m^2 ha^{-1} for the control on the same site.

Deployment in the WA FPC developed in a different direction from the rest of STBA (and independently since 2000). In addition to vegetative propagation as described above, the hedged orchard concept proposed by Sweet and Krugman (1978) was adopted and further developed. Butcher (1986) termed such orchards as HAPSO (hedged artificially pollinated seed orchard). Two populations have been defined for HAPSO production, both having selection traits of high growth, stem and branch form and wood density and one having the additional trait of tolerance to *P. cinnamomi.* These populations were also subdivided on the basis of parental origin of the original plus trees for inbreeding control. Operational development of HAPSOs was a significant achievement and involves control of pollination using chemical emasculation and careful management of the hedgerows (Tan and Butcher 1988).

Although radiata pine is a minor plantation species in Queensland (1192 ha in 2000 (Wood *et al.* 2001)), deployed in a few southern, higher-elevation, summer- or uniform-rainfall areas, a modest breeding effort was maintained from the late 1940s until the early 2000s. Progeny testing began in 1950 of trees selected for, among other criteria, putative tolerance of the fungus *Diplodia pinea* (syn. *Sphaeropsis sapinea*), a strong constraint on productivity of the species in Queensland. Some 15 of the best New Zealand selections, including the famous NZ55, were imported as grafts in the 1950s and later crossed with local selections. Grafted seed orchards were established using first- and second-generation selections (including some selections in the progeny of New Zealand × local crosses), and local, improved seed was available from the mid-1960s. A seed orchard planted in 1981 with seedlings of 89 bulk seedlots from the ACT, NSW, Victoria, New Zealand and local breeding programs contributed further diversity of propagation populations. Queensland also participated in a number of collaborative trials. Results demonstrated superiority of some non-local sources, especially New Zealand. In view of this and the small area of deployment (the species was replaced in most areas), local breeding work ceased in the early 2000s. Now, rooted cuttings of high-merit families sourced from New Zealand through NSW are used in the small-scale, ongoing deployment program that is in the wettest and highest-elevation area only (Haley 1957, 1960; Garth Nikles, *pers. comm.* 2007).

[2]Butcher, T.B. (2003) Improvement of drought tolerance of commercial tree crop species. National Heritage Trust, Project Final Report. NHT Project FFP 983194.

Radiata pine breeding and research highlights

CSIRO, the Forestry and Timber Bureau (CSIRO forestry's predecessor), the STBA, Forests NSW, the WA Forests Products Commission and other collaborators have achieved a great deal in radiata pine breeding over the last 50 years or so. Now large areas of commercial plantations, established using genetically improved seeds and cuttings, have growth rates and log quality superior to those of the earlier plantations established with unimproved seeds. Numerous publications detail the achievements, of which the following are particularly outstanding:

- The establishment of the first radiata pine seed orchard in 1957 at Tallaganda, NSW, was a milestone for radiata pine breeding (Eldridge 1982). As well as seed for plantations, this orchard provided seed for several significant genetic studies. By the early 1980s, most Australian radiata pine plantations were being established using seed from this and other orchards.
- Wide adoption of cuttings in the mid-1980s as the practical result of 40 y research on vegetative propagation of radiata pine by scientists of CSIRO and its predecessors (Fielding 1970; Brown 1974) and of more recent work on identification of superior families for mass vegetative propagation (cuttings from hedged seedlings of selected control-pollinated families).
- A genotype × environment experiment established between 1969 and 1970 on 11 sites across six states and the ACT. This series of trials used 30 open-pollinated families selected from Australia and New Zealand before 1960. The results indicated that one breeding zone was sufficient for site conditions represented by the trial sites (Matheson and Raymond 1984).
- Seed collection from the five radiata pine native populations in 1978 resulted in large-scale provenance trials. Six scientific seed collections were recorded before 1978. The 1978 collection of five native populations (Eldridge 1978) was by far the largest in terms of number of families, completeness and quantity of seeds. More than 100 trials were established within Australia and worldwide. This collection has generated significant information on population dynamics and genetic variation, and will guide and provide material for long-term ex situ genetic conservation and refreshment of the current breeding population via infusions (Eldridge 1997).
- Development of a nucleus breeding strategy for radiata pine. Cotterill *et al.* (1989) introduced the concept of the nucleus breeding strategy into tree breeding and advanced it in the radiata pine breeding program. The nucleus breeding strategy focuses on efficient selection for additive genetic variance by rapid improvement of a small elite nucleus population (Cotterill and Dean 1990). This strategy has been adopted in some other tree breeding programs (Joyce 1993).
- An Australia-wide diallel mating experiment. From 1976 to 1987, as a member of Research Working Group 1, CSIRO organised a large-scale diallel mating experiment to advance

radiata pine breeding from the first to the second generation. A total of 21 disconnected sets of 6 × 6 half-diallel crossing systems (i.e. all crosses among six parents excluding reciprocals and selfs) were made by RWG1 members and planted on ten sites across four states in the 1980s. These genetic trials have generated significant information that will guide future radiata pine breeding. A separate deployment population has been proposed for high-altitude sites based on the discovery that a large genotype × environment interaction is elicited by such environments. It was found that sizable non-additive genetic variation could be used in radiata pine breeding and deployment populations (Wu and Matheson 2004, 2005), for example by clonal forestry.

- An inbreeding experiment. This long-term study (from the 1960s to the present) indicates that (a) genetic load is low in radiata pine, (b) purging deleterious alleles through inbreeding is effective in radiata pine, and (c) selfing and subsequent outcrossing could be a more efficient breeding method for radiata pine than conventional population improvement (Wu *et al.* 1998, 2004a).
- Genetics of wood quality. A series of quantitative genetics studies was conducted for wood quality traits in radiata pine, from basic density to end-product quality (Matheson *et al.* 1997; Nyakuengama *et al.* 1997). These studies were instrumental to an understanding of the importance of wood quality traits in radiata pine improvement.

Economic benefits of radiata pine genetic improvement

Genetic improvement of radiata pine by CSIRO, STBA and other collaborators has generated significant economic benefits for Australian forest industries. An independent economic evaluation (Sullivan 1999) found that Australian investment in radiata pine breeding to 1999 had a net present value of A$927 million, through increased productivity and quality of the plantations produced. Realised genetic gain up to 33% was reported for volume at age 15 y from first-generation selections in one seed orchard (Matheson *et al*. 1986, 2002). Most first-generation gain trials measured at ages of 10–15 y indicated an average of 20–25% volume gain (Eldridge 1982; Johnson *et al.* 1992). There is also a trend for gain to increase with age. An internal rate of return of 20% was estimated as the economic return from first-generation breeding (Wright and Eldridge 1985). Boomsma (1992) suggested that the best control-pollinated families could produce about 23% gain on top of about 24% gain from rogued seed orchard (G1.5) on a site of average 'quality IV' in Mount Gambier. There are also additional gains from organic matter conservation, nutrients (use of fertiliser) and moisture conservation (control of weeds). Predicted genetic gains for the second generation in diameter of 4–17% indicated a volume gain of more than 10% (White *et al*. 1999; Wu and Matheson 2005).

Recent focus of radiata pine breeding

Many factors affect the outcome of any tree breeding program. After two generations of breeding, it was realised that at least four fundamental and practical research investigations were required for further progress in this work.

The first and most important requirement was better definition of the breeding objective, which should aim to improve the profit of the forest enterprise rather than individual biological traits, particularly in dealing with negative genetic correlations between quantity (typified by volume) and quality traits (typified by density and stiffness).

The second requirement was an efficient information management system combined with accurate prediction of breeding values. The STBA radiata pine breeding program currently has access to tree breeding data for more than 500 000 trees and associated genetic material that has been developed over a 50-y period by CSIRO, STBA and radiata pine growers. Data on thousands of trees growing in current trials are also being captured. Information management becomes a considerable task as it includes data input, retrieval, compiling, inquiry, statistical analysis, prediction of breeding values, management of germplasm, and delivery of information to breeding members. An accurate prediction of genetic (breeding) values for trees in the breeding population is fundamental to the success of any advanced tree breeding program with data from multiple generations, pedigrees, sites, ages and traits. The optimal statistical method for predicting breeding value is the best linear unbiased prediction (BLUP). Therefore, one priority for the radiata pine breeding program was to develop a BLUP system that suited radiata pine and other tree breeding programs.

Thirdly, with the development of BLUP-based software packages to perform genetic analysis and to predict breeding values came recognition that changes to the breeding strategy were required to take advantage of the advances in genetic analyses and prediction of breeding values.

Fourthly, investment in genomics and biotechnology in tree genetics was needed, and many alleles for important quantitative traits are being identified using gene discovery and association genetics. This has prompted new research into the integration of genomics and biotechnology with practical breeding. These new research projects for the STBA radiata pine breeding program are summarised below.

Breeding objectives

The most important aspect of a tree breeding program is the definition of an appropriate breeding objective. Ideally the objective will be clearly defined in economic terms, and it must be based on traits that are under genetic control and influence the profit of forestry enterprises. In recent years, the radiata pine breeding program has been based on the improvement of four traits — harvest volume, whole-tree density, stem form and branching (Powell *et al.* 2004). These were combined in an index that allowed the radiata pine industries to select genotypes based on their predicted overall genetic merit for these traits. Until 2005, only arbitrary economic weights of the four breeding objective traits were available to use in the index.

In a recent collaborative project between CSIRO and STBA, economic breeding objectives have been precisely defined and developed. The results show that a significant proportion of future genetic progress is likely to come from improving wood quality traits such as stiffness, rather than from higher growth rates

(Ivković *et al*. 2006a). The optimal economic weights for breeding objective traits were developed through the following six steps:

1. Defining three production systems (plantation grower, sawmill and integrated companies) for radiata pine solid wood production (see Table 2).
2. Defining four breeding objective traits for production systems: MAI — mean annual increment measured as m^3 ha^{-1}; SWE — stem sweep measured as maximum deviation of log axis from a straight line over the log length in mm m^{-1}; MOE — modulus of elasticity, measured as stiffness of clearwood in GPa; and BIX — branch size index, measured as the maximum diameter of branches in four quadrants of a log in cm.
3. Developing a bio-economic model and estimate economic weights for the four breeding objective traits (Ivković *et al*. 2006a).
4. Estimating genetic parameters to link early selection and breeding objective traits (Wu *et al*. 2004b).
5. Estimating selection indices for three the types of radiata pine enterprises (see 1 above).
6. Studying the sensitivity of estimates of economic weights and selection indices to economic, biological and genetic parameters in a bio-economic model (Ivković *et al*. 2006b). The estimated gain in net present value (ΔNPV) based on selection using the economic index can be estimated from the economic model (Table 2). Gains for NPV between 35% and 85% are predicted to be achievable for a selection intensity of 10% based on the index.

Information management and genetic evaluation systems

Three basic tools are crucial to effectively managing an advanced tree breeding program. They are:

- a data management system
- a genetic evaluation system
- a crossing and deployment management system.

Over the last 6 y the STBA has developed a relationship-based data management system — the STBA-DMS™. This employs a Web-based interface that makes possible access to information from multiple diverse sites. The system has allowed the rapid updating of genetic values and their dissemination to users; it not only stores performance data but also manages pedigree for genetic evaluation purposes. This gives the ability to track pedigree both for use in genetic evaluation and for general purpose use in crossing programs, trial measurement, assessment, etc. WA FPC has also recognised the same need and developed a Dbase program, TBIMS (Tree Breeding Information Management System), to keep track of its genetic resources.

BLUP-based software called TREEPLAN® has also been developed for genetic evaluation of large data sets from the STBA radiata pine program and for other species (McRae *et al.* 2003). TREEPLAN®, which is integrated with the STBA-DMS™, has been operating since 2002 to manage the radiata pine genetic resource. The STBA-DMS™ efficiently manages progeny trial data, making information available across the internet for day-to-day management purposes, and it also provides structured data for genetic evaluation by TREEPLAN®. The STBA-DMS™ also holds the results from TREEPLAN® runs; these too are available via the internet.

Powell *et al*. (2004) summarised the procedures and methods used in estimating genetic values for trees in the STBA radiata pine breeding population. As an example, breeding values for the four previous breeding objective traits volume, density, branch size (on a scale of 1 to 6, 6 is the smallest branch) and stem straightness (on scale 1 to 6, 6 is the straightest stem) for each genotype (tree) were predicted by using data on 134 676 trees from 78 sites. These breeding values have been combined into a selection index. Table 3 shows the average of breeding values predicted for the top 20, 100, 1000 and 10000 genotypes for each breeding objective trait as well as for the combined index, with selections variously based on the index and each of the four breeding objective traits. For example in the first line of Table 3, if the top 20 trees out of 134 676 were selected using this index, there will be expected genetic gains over a rotation of 134 m^3 ha^{-1}, 0.70, and 0.12 for volume, branch score and stem straightness, respectively, but a loss of 17 kg m^{-3} for wood density, relative to the whole population mean (base productivity).

New breeding and deployment strategy

With the use of BLUP in genetic evaluation, it was recognised that significant changes in the strategy were needed to increase

Table 2. Estimated genetic response in breeding objective traits and predicted genetic gain in net present value from index selection for three different production systems[1]

	Breeding objective traits				
	MAI (m^3 ha^{-1})	SWE[2] (mm m^{-1})	BIX[2] (cm)	MOE (GPa)	ΔNPV (%)
Present mean	24.0	10.3	5.5	11.3	
Production system					
Grower	8.09	0.37	–0.63	0.02	85
Sawmill	2.21	–4.40	–0.31	0.32	35
Integrated	6.70	–2.07	–0.57	0.15	57

[1] For a selection intensity of 10% (i = 1.755)
[2] Expressed as metric size, where smaller is better

Table 3. Mean index and breeding values for selection based on index selection or individual breeding objective trait under varying selection intensities[1,2]

Base productivity[3]		INDEX	VOLUME 500 m^3 ha^{-1}	DENSITY 400 kg m^{-3}	BRANCH 3.5	STEM ST 3.5
Selecting best based on INDEX	Top 20	220.81	134.10 (27)	–17.04 (–4)	0.70 (20)	0.12 (3)
	Top 100	205.62	126.63 (25)	–15.37 (–4)	0.60 (17)	0.16 (5)
	Top 1000	177.98	103.14 (21)	–13.04 (–3)	0.52 (15)	0.22 (6)
	Top 10000	133.72	1.70 (14)	–10.75 (–3)	0.42 (12)	0.20 (6)
Selecting best based on VOLUME	Top 20	199.81	155.97 (31)	–28.35 (–7)	0.34 (10)	0.17 (5)
	Top 100	186.54	143.00 (29)	–24.32 (–6)	0.34 (10)	0.15 (4)
	Top 1000	157.24	119.07 (24)	–19.79 (–5)	0.28 (8)	0.15 (4)
	Top 10000	109.79	86.39 (17)	–13.14 (–3)	0.19 (6)	0.06 (2)
Selecting best based on DENSITY	Top 20	–24.07	–29.41 (–6)	45.18 (11)	–0.02 (–1)	–0.09 (–3)
	Top 100	–13.40	–29.32 (–6)	35.56 (9)	0.06 (2)	–0.04 (–1)
	Top 1000	–9.45	–18.03 (–4)	24.79 (6)	0.01 (0)	–0.01 (0)
	Top 10000	0.76	–8.35 (–2)	15.04 (4)	0.02 (1)	0.02 (0)
Selecting best based on BRANCH	Top 20	123.12	11.54 (2)	–7.41 (–2)	1.13 (32)	–0.28 (–8)
	Top 100	116.74	9.29 (2)	–6.75 (–2)	1.03 (29)	–0.17 (–5)
	Top 1000	109.73	18.95 (4)	–5.10 (–1)	0.85 (24)	–0.11 (–3)
	Top 10000	97.16	27.90 (6)	–3.81 (–1)	0.60 (17)	–0.02 (0)
Selecting best based on STEM	Top 20	90.75	26.87 (5)	–3.17 (–1)	–0.05 (–1)	0.92 (26)
	Top 100	89.17	27.85 (6)	–5.13 (–1)	–0.02 (0)	0.84 (24)
	Top 1000	76.91	25.11 (5)	–5.59 (–1)	0.00 (0)	0.70 (20)
	Top 10000	64.91	24.74 (5)	–3.93 (–1)	0.02 (1)	0.50 (14)

[1] Numbers in parentheses are percentage genetic gain or loss
[2] Results derived from TREEPLAN run PRAD2004 October 2004
[3] Base productivity values for traits in the column headings are means for the whole population (134 676 trees)

the rate of genetic progress. Some of the specific changes adopted or contemplated are:

1. Replacing discrete nucleus and main breeding populations by a single breeding population. (Nucleus–Main breeding was largely developed for animal breeding in situations that are different to those found in radiata pine). However, independent breeding sub-lines will continue, at least in the short-term. This aids in managing inbreeding and ensures deployment populations are outcrossed.
2. Replacing discrete generation breeding with rolling front breeding (Borralho and Dutkowski 1998). This is expected to lead to operational efficiencies, increased selection pressure, earlier adoption and use of elite genotypes for breeding, easier infusion of new material, reduced risk, better accounting of genotype × environment interaction — all of which lead to enhanced gains. TREEPLAN® genetic evaluation has facilitated the adoption of the rolling front strategy.
3. Reducing the size of the breeding population (340) and managing effective population size using a 'selection and mate allocation' genetic algorithm under development.
4. Developing separate deployment 'breeds' with two sub-lines per breed. In the interim, three breeds (Multi-purpose, Density–Growth and Growth–*Phytophthora* resistance) will continue to be used for breeding.
5. Using deliberate inbreeding to purge recessive alleles to alleviate the long-term inbreeding issue (Wu *et al.* 2004a).
6. Infusing genes (Fig. 2) via the inclusion of new, local selections from within plantings of the 1978 range-wide seed collections of Eldridge (1978). This may be necessary as the genetic base narrows progressively over generations of recurrent selection.

This new strategy for the third generation of selection and mating under the STBA has changed the way that tree breeding is conducted. This is a dynamic strategy with overlapping generations, and breeding values of individual genotypes that may change from year to year as new data accumulate. This is in contrast to discrete generation breeding for which breeding values usually remain static for a full generation. Two significant issues for STBA radiata pine breeding are inbreeding within breeding and deployment populations for a single advanced breeding population, and the relatively narrow genetic base of the breeding population. The STBA radiata pine breeding population is significantly different from other pine breeding populations in the world because original plus trees were all selected from plantations, which may themselves have originated from a population of small effective size due to bottleneck and founder effects. For these reasons, deliberate inbreeding and genetic infusion of radiata pine breeding populations should be critical components of breeding strategy.

Integration of molecular genetics with breeding ('Juvenile Wood Initiative')

Improvements of growth rate in radiata pine over the first two generations of breeding, in combination with improvements in silvicultural practices, have contributed to a decrease in rotation age in Australia from around 40–45 y to 27–30 y. One unwelcome effect of shorter rotations and more rapid early growth is that the proportion of the relatively weak juvenile corewood in harvested logs has increased and, as a result, overall wood quality has declined due to adverse changes in wood properties — lower density and stiffness, shorter fibres, lower cellulose content and higher incidence of knots. For these reasons the focus of radiata pine breeding from the third generation on has shifted to wood quality traits. In 2003, CSIRO in partnership with STBA, the Queensland Department of Primary Industries Forestry (QDPIF) and the Forest and Wood Products Research and Development Corporation (FWPRDC, now Forest and Wood Products Australia, FWPA) and ArborGen (a US based tree biotechnology company) began work on the 'Juvenile Wood Initiative' project covering radiata and the slash × Caribbean hybrid pines. This project aims to significantly increase the value of Australia's pine wood production by reducing the proportion of juvenile wood produced in each tree (decreasing the age of transition from juvenile wood to mature wood) and by improving the quality of the wood (for example, increasing the inherent stiffness of the juvenile wood) through integration of quantitative genetics, molecular genetics and biotechnology.

Two of the early goals for the Juvenile Wood Initiative were finding the best method to screen standing young trees for stiffness and to sample for basic density in a number of progeny trials that form the core of the STBA radiata pine breeding program (Wu *et al.* 2007a). By the end of 2004, the project had sampled over 7000 trees for wood increment cores from six of these trials, consisting of elite advanced genetic material, and incorporated the results into the 2004 TREEPLAN® run. Selection of the best 250 trees would produce an estimated 12.4% increase in wood density. In another assessment, selection of the best 10% of trees from over 3000 for acoustic 'time-of-flight'-based stiffness would result in an estimated 21% genetic gain in stiffness. This would represent a significant improvement in wood quality and have an immediate impact on the ability of STBA members to select genotypes with improved wood stiffness for deployment. It was found that the best method to predict stiffness of a standing tree in both radiata and slash/Caribbean pine is to use gravimetric basic density from a 12 mm increment core at breast height combined with a standing tree prediction of MoE using a time-of-flight acoustic tool.

The project also created the first radiata pine 18 k cDNA microarray and discovered numerous candidate genes differentially expressed in juvenile wood formation and in trees with high and low stiffness. By the end of 2006, more than two thousand SNPs (single nucleotide polymorphisms) responsible for juvenile wood formation had been discovered (Dillon *et al*. 2007) and the inheritance of traits related to juvenile wood quality (density, microfibril angle, modulus of elasticity, spiral grain, shrinkage, juvenile–mature wood transition, etc.) were better understood (Li and Wu 2005; Gapare *et al*. 2006, 2007; Matheson *et al*. 2007). Analyses of genetic correlations between growth and density in juvenile wood from a series of trials indicated a large and significant adverse correlation between diameter and wood density (Baltunis *et al*. 2007), consistent with other studies (Wu *et al.* 2007b), indicating that coping with or overcoming such adverse correlations will be a technically challenging task.

Conclusion

The successful introduction and domestication of the exotic radiata pine in Australia is an excellent example of tree plantations becoming the base for a new forest-based industry with a significant role in mitigating the crisis in national forest resources supplies and deterioration of the environment. The initial introductions of radiata pine about 1860, which were for ornamental and mine-rehabilitation plantings, came from two of the five natural populations and were the sources of the current large plantations. It appears that the original genetic base may have been of the order of 200–300 seed trees from a small part of the natural range of this variable species. Various other bottleneck or founder effects — through constrained seed collections from ornamental and windbreak plantings for earlier commercial plantations — may have further eroded genetic diversity of the breeding population. The ex situ conservation plantings from the 1978 range-wide collection could provide much greater genetic diversity for future breeding populations.

The substantial genetic gain in growth and form achieved from selection and breeding since the late 1950s has resulted from gradual introduction of the most advanced breeding tools and methods for population improvement. The cooperative breeding program of the STBA, now in the third generation of breeding, focuses on wood quality, integrates quantitative genetics and molecular genetics, uses full-sib progeny testing and BLUP to predict breeding values through TREEPLAN®, and has developed the STBA-DMS™ to manage large, complex and pedigreed databases. Deployment is through control-pollinated seed orchards together with mass vegetative propagation by rooted cuttings of superior families. To ensure genetic sustainability and further increase genetic gain, the following actions are critical:

- infusion of new genetic material from the range-wide collections
- purging of inbreeding depression
- increasing recombination rate and selection intensity
- fully exploiting non-additive genetic variation by clonal forestry
- developing strategies dealing with adverse genetic correlations between wood volume and quality traits.

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