

## 6 Radiata pine tree-breeding

Radiata pine has proved to be very adaptable to domestication. It is easy to propagate and grow using a wide range of silvicultural techniques on a variety of sites. This adaptability to domestication and the species' inherent genetic variability are two reasons for the rapid genetic improvement that has been achieved in radiata pine. The third ingredient for a successful breeding programme is also present in several countries: the commitment to a large planting programme coupled with an intensive research effort. This commitment has also been present in some countries for several other major plantation species, such as the southern pines, some eucalypt species – particularly hybrid eucalypts – and rubber, as well as for some minor plantation species, such as Douglas fir. However, advanced tree-breeding is not as rewarding for species grown in natural forests or for very slow-growing species.

In New Zealand and Australia, tree improvement in radiata pine began in the 1950s, with the planting of the first seed orchards in 1957 (Shelbourne *et al.*, 1986; Wu *et al.*, 2007). The early efforts aimed to improve growth rates and tree form and, by the 1980s, seed orchards were producing most of the seed needed by growers. The South African radiata pine tree-breeding programme started in 1961. In Chile, tree-breeding began in the late 1970s and also focused on growth rates and tree form. There is a university–industry radiata pine breeding cooperative in Chile. A breeding programme was launched in Galicia, Spain, in 1992.

### IMPROVEMENT OBJECTIVES

Establishing the goals of a tree-breeding programme needs careful thought. Not only must the biological potential of the species be considered, its long-term market requirements also need to be evaluated. For some characteristics, this may be difficult because industrial processes and market preferences are subject to continual change. Silviculturists also face this when making other decisions, such as whether to high prune. However, the problem is compounded for the tree-breeder because changes in the genetic make-up of a tree are slower and more expensive to obtain, are potentially permanent and may be difficult to retrieve if a mistake is made. The time factor also dominates tree-breeding decision-making, since the key tree-breeding objective is to obtain the maximum gain per unit of time (Zobel and Talbert, 1984). At the same time, it is necessary to be aware that the land base for radiata pine plantations may change, that the future plant growth environment is likely to be affected by climate change, and that other forms of silviculture can sometimes achieve similar ends.

Despite these difficulties, it is generally possible to decide on reasonable tree-breeding objectives. These do, however, tend to concern those traits that will generally be desirable no matter what the end use and to allow a flexible breeding strategy. Thus, for most purposes, fast growth, stem straightness, a lack of malformation, good wood properties and resistance to common diseases are important factors in tree-breeding programmes (Zobel and Talbert, 1984; Burdon, 2001). Current radiata pine breeding programmes emphasize these traits because the focus is on improving the species for wood production. There has been no interest in improving the species for amenity or soil conservation values, partly because growers can either use existing breeds or other species to fill these roles. However, there is interest in breeding for some nutrient-deficient sites.

Five factors need to be heeded when setting tree-breeding goals:

- There is usually a need to breed for several traits. These are unlikely to be of equal value and may be uncorrelated or positively or negatively correlated. Including more traits in the tree-breeding programme will reduce the rate of gain made in any one trait.
- Perceptions of the most important traits change over time. The increasing disease load has become one of the biggest problems facing growers of radiata pine (see Chapter 4), and breeding is considered a strategy against these threats. Similarly, wood properties were initially given low priority but are now considered important (Sorenson, 2007).
- The tree-breeder also needs to grapple with specific requirements such as special sites or distinctive end uses. Until recently, breeders have usually aimed to develop genotypes that are satisfactory for a wide range of conditions, but there is growing interest in developing specific breeds for some site types and a mix of end-use product characteristics (Carson, 1996).
- Goal-setting is also related to propagation and possible breeding techniques. Recent developments in micropropagation and somatic embryogenesis methods and in seed orchard design are providing greater flexibility in future breeding objectives (Walter *et al.*, 1997). New biotechnology techniques may also offer opportunities. New Zealand scientists have already inserted genes that make radiata pine more resistant to some insect pests, although these genotypes are yet to be deployed commercially, and they are also researching the use of gene markers (Grace *et al.*, 2005; Burdon and Wilcox, 2011).
- The relationship with other silvicultural methods and other management options aimed at achieving the same ends must be considered. To improve wood flows, for example, the forest manager may resort to options such as buying wood, applying fertilizer, thinning to prevent losses from mortality, planting new areas, or tree-breeding. An advantage of tree-breeding is that it provides long-term gains without the need for further interventions. Note, however, that the time to achieve the objective differs between options, the longest time being for tree-breeding (Mead, 2005a). Also, there is often synergism between tree-breeding, intensive silviculture and wood quality. For example, improving bole straightness enables the use of lower initial stockings, makes for easier thinning, reduces extraction costs and gives higher sawmill yields.

In Australasia there is now a push to redefine tree-breeding goals in the wider context of site, silviculture and end use (Box 6.1). Ultimately, the aim is to match genetic ideotypes (distinct breeds) with site characteristics and end use, propelled in part by the continuing development of clonal forestry. This foreshadows the full domestication of radiata pine, which has occurred in other crops.

## BIOLOGICAL BACKGROUND

Radiata pine usually does not begin to bear mature female cones until it is about eight years old, although the actual age is partly dependent on the individual genotype and planting site (see Chapter 5). The serotinous cones take about three years after initiation and about two years after pollination to reach full maturity. These factors influence breeding plans and the rate of improvement.

Successive female clone clusters, which are modified shoots, are associated with the polycyclic nature of the species, so that cones may become receptive to pollen over a period of five or more weeks in spring (Lill and Sweet, 1977; Sweet *et al.*, 1992; Madgwick, 1994). Generally, an individual cone is receptive for 2–13 days and the ovules (female cells that could develop into seeds) are pollinated by several pollen grains. However, only one of these embryos will develop into a seed; the others abort. Under natural conditions, the movement of pollen to the ovule micropyle is dependent on either a pollination droplet or rain. It is also possible to manually apply pollen in

a liquid with the aim of achieving this rapid transfer, thus preventing most unwanted pollination from outside sources (Sweet *et al.*, 1992).

The male strobili, which in radiata pine are produced from around age five years, are modified short shoots (fascicles) and are most numerous on the lower crown branches. Pollen is wind-distributed in spring, but, if required, it is easily collected and dry pollen may be stored for several years at temperatures well below freezing point. This is important for control-pollinated seed orchards.

There is commonly a 50 percent loss of female cones in the first year after pollination, although it can be as high as 90 percent. These losses occur 4–6 weeks after receptivity and appear to be partly related to rapid shoot extension and a lack of pollination, although frost and other biotic factors are sometimes important. Intensive silvicultural practices such as irrigation or nutrient applications have not proved advantageous

#### BOX 6.1

##### **The changing breeding goals for radiata pine: an example from Australasia**

Early on, breeders of radiata pine concentrated on vigour and, above all, tree form. Selection focused on non-malformed, straight, fast-growing trees with small flat-angled branches (as found with polycyclic trees). Selection for wood properties, such as wood density and spiral grain, was largely ignored, even though it was recognized that they were highly heritable traits. Industry largely concurred with this decision. One of the genetic problems was that there was a negative correlation between growth rate and density. The consequence of these breeding goals was that wood density dropped in favour of higher growth rates. Seed from these orchards had gains in stem volume of about 20 percent and increased the percentage of acceptable stems from 45 to 70 percent.

Silviculture in Australia and New Zealand was undergoing a revolution at about the same time. Rotation lengths were reduced substantially in both countries – especially in New Zealand and Western Australia. Partly because of the greater number of acceptable trees, initial planting stockings were reduced and in many cases precommercial thinning and pruning were undertaken. Weed control improved and often former pastures were replanted, again increasing early growth rates. The outcome was that the amount of low-density corewood (juvenile wood) increased substantially and became a major problem for sawmills. By the late 1980s, New South Wales foresters had decided that corewood density should be incorporated as a breeding goal.

Research on wood properties has led to greater understanding of corewood properties and to the identification of alternative breeding traits such as microfibril angle and spiral grain, as well as wood density. Acoustics can now be used to measure wood stiffness. The size of the corewood zone can be reduced appreciably by breeding. Economic studies have confirmed that more emphasis should be given to improving wood quality. Disease resistance has also become a more important goal.

The development of techniques such as the mass multiplication of seedlings and micropropagation has allowed the multiplication of top genetic material. Cryopreservation and embryogenesis have enabled the development of clonal forestry, which makes it possible to capture non-additive variance and to breed specific varieties for different sites, end uses and silviculture. In essence, this means exploiting the genetics x site and genetics x silviculture interactions. Using clones can also speed up the breeding programme and allow tree-breeders to select genotypes that break adverse correlations such as growth rate and wood density. It also brings reduced variability when clones are deployed as mosaics, compared to seedlings, thus providing a more uniform product. The improvement goals are changing as a result of these new technologies.

in either preventing abortion or increasing seed production in radiata pine (Sweet and Hong, 1978; Madgwick, 1994). However, the selection of a seed orchard site is important, with the most productive places having hot, dry summers and low site quality in terms of vegetative growth. The application of gibberellins (a type of plant hormone) can increase flowering by two-thirds and has been used in most radiata pine control-pollinated seed orchards (Sweet, Bolton and Litchwark, 1990).

Some 13 months are required following pollination before the ovules are finally fertilized. With subsequent development, food reserves accumulate in the endosperm and the seed coat hardens; maturation leads to seed dehydration. As the cones dry they turn brown. However, this maturation time may be shortened by picking the cones 18–20 months after pollination and ripening under controlled conditions – that is, in early winter, almost one year prior to the autumn in which they are expected to first open naturally (Rimbawanto, Coolbear and Firth, 1988). This procedure has been used commercially, although in New Zealand there is a move towards allowing the cones to ripen on the tree.

Like most conifers, radiata pine has a very large genome and this inhibits complete genome sequencing and makes it difficult to find important genes or gene sequences that are markers of important traits. Despite this, some progress has been made in identifying genetic markers (Burdon and Wilcox, 2011).

### THE QUANTITATIVE GENETIC APPROACH

Most traits that breeders wish to alter in trees are controlled by multiple genes, so the variation in such traits follows an approximately normal distribution. Tree-breeders therefore tend to base their approach on the quantitative study of variances (Zobel and Talbert, 1984).

Total phenotypic variance ( $V_p$ ) for a trait (i.e. what is observed in the field) is made up of a genetic ( $V_g$ ) and an environmental component ( $V_e$ ) and their interaction ( $V_{ge}$ ):

$$V_p = V_g + V_e + V_{ge}$$

The proportion of the genetic and environmental components varies widely between traits. Diameter, for example, has a large environmental component, whereas wood density is largely controlled by genetics. Thus, wood density has a relatively high heritability compared with diameter (Table 6.1).

The importance of the genotype–environment interaction in breeding programmes for radiata pine is still under debate. For example, Spanish researchers suggest that for most traits it is possible to select trees that show good combining ability and that therefore there is no need to exploit genotype x site interactions (Codesido and Fernández-López, 2009), although they suggest that exploiting genotype x site interaction would be worthwhile for frost resistance. With the development of clonal forestry it is becoming easier to target gains for specific sites and traits (Carson, 1996; Carson and Carson, 2011). However, with traditional breeding programmes based around seed production in seed orchards, the additional gains to be made by using genotype–environment interactions is often small in relation to the effort required (Carson, 1991). For genotypes to be matched to the environment, the environment must be well-defined and repeatable.

The genetic variance ( $V_g$ ) may be broken into two main parts: additive and non-additive (Zobel and Talbert, 1984). When individual parents pass on traits in combination with any other parent, this is termed their general combining ability, and it reflects the additive genetic variance ( $V_a$ ). Narrow sense heritability ( $b^2$ ) is the proportion of the additive to total variance, and is used to estimate breeding value. However, some individuals may show dominance and epistasis due to the non-additive component ( $V_{na}$ ). The specific combining ability reflects this non-additive part and is determined by studying the performance of individual crosses. Broad-sense heritability ( $H^2$ ) is the combined additive and non-additive components (i.e.  $V_g$ ) as a proportion of

TABLE 6.1  
Estimated heritabilities ( $h^2$ ) for a range of radiata pine traits

Trait	Heritability	Coefficient of variation (%)
Height	0.2	12
Diameter	0.1–0.3	15
Stem straightness	0.1–0.4	
Branch clusters	0.35	20–30
Branch size	0.27	
Branch angle	0.2	
Root regeneration (seedlings)	0.3	
Wood density	0.6–0.8	5–10
Acoustic velocity	0.4	10
External resin bleeding	0.3–0.4	50
Longitudinal shrinkage	0.3	35–50
Spiral grain	0.55	
Tracheid length	0.54	
Stiffness	0.5	
<i>Dothistroma</i> defoliation	0.3	
<i>Cyclaneusma</i> needle-cast	0.1–0.35	
<i>Fusarium</i>	0.3–0.8	
<i>Essigella</i> defoliation	0.2–0.5	
Mg deficiency	0.7	
Drought resistance	0.1	
Frost resistance	<0.2	
Wind damage	0.05	

Sources: Madgwick, 1994; Burdon, 2001; Beets *et al.*, 2004; Kumar, Burdon and Stovold, 2008; Ivkovi *et al.*, 2009; Wu *et al.*, 2008

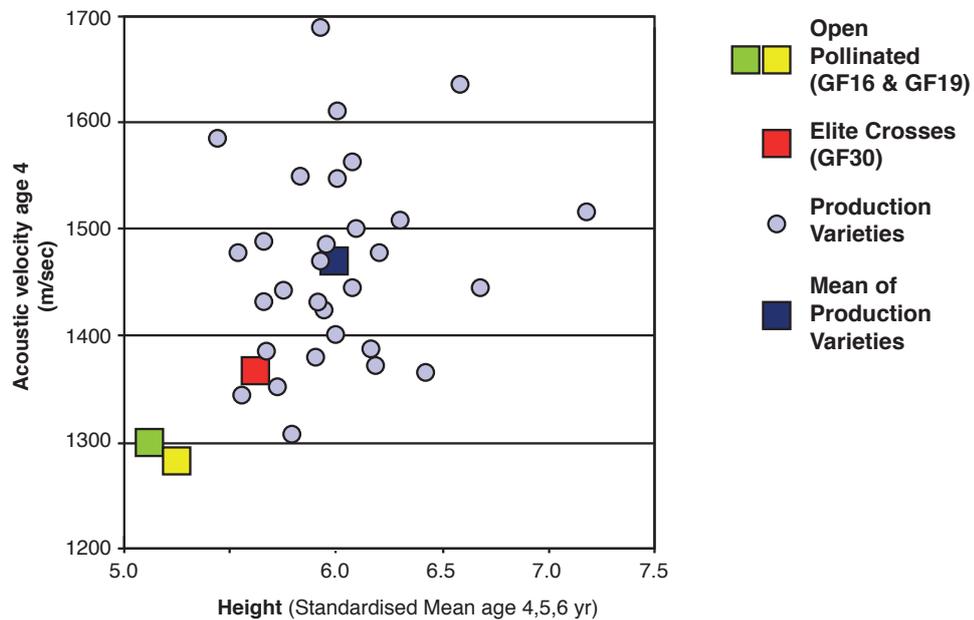
total phenotypic variability. While most breeding in radiata pine has revolved around pursuing general combining ability, one potential advantage of using clones is that the non-additive genetic variances can be captured and this can lead to larger gains (Figure 6.1).

Breeders select above-average individuals for that trait and the difference between the mean of the selected group and the population average is the selection differential. Genetic gain (G) from seed orchards is the product of the selection differential and the narrow sense heritability and is usually expressed as the percentage gain. For clonal selection, G is the product of the selection differential and broad-sense heritability.

For most characters of interest in radiata pine it is appropriate to use reasonably high selection intensities. In the early years (1953–1958), the selection intensity in New Zealand was very high (selecting one tree per 100 ha or 1 in 25 000 from 30-year-old, land-race stands) and produced a relatively small number of plus-trees for potential use in clonal seed orchards (Burdon, Carson and Shelbourne, 2008). In light of selection theory, however, a second cycle of selections of many more plus-trees was made in New Zealand in 1968. These were from 12–18-year-old stands, with the selection intensity reduced to about one tree per 1.2 ha (1 in 400 trees). This was followed by comprehensive progeny testing and further selection.

Genetic gain depends on the availability of moderate to high heritabilities and a useful amount of genetic variation. The heritabilities (Table 6.1) of different traits vary widely for radiata pine. Some characters are highly heritable and large gains can be

FIGURE 6.1  
The use of selected clonal varieties can simultaneously improve both acoustic velocity (i.e. wood stiffness) and growth rate



Note: The seed orchard trees from open-pollinated orchards (green and yellow) were inferior to control pollinated seed (red), while the selected clones were often better in both characteristics. Source: M. Carson, personal communication, 2012 (see also [www.forest-genetics.com/pine-trees/pine-trees-pages/tree-performance.aspx](http://www.forest-genetics.com/pine-trees/pine-trees-pages/tree-performance.aspx))

made through an initial plus-tree selection. Other traits have low heritabilities and it is necessary to test how their progeny perform relative to others to obtain acceptable gains. This is called “backward selection” (because the breeder looks backward to see which parental selections performed best), in contrast to the “forward” direction of a phenotypic selection. The phenotype is simply the sum of the features or traits observed in a tree.

Quantitative tree-breeding, the basics of which were introduced above, should take into account the following complicating and practical factors:

- Simultaneous selection for several traits results in less improvement in any one trait (multitrait selection methods are discussed later).
- The correlation between traits may be positive, negative or nil. For example, it is difficult to select for both long-internode trees and high growth rate in radiata pine or for both high growth rate and wood density (Carson, 1986; Sorrenson, 2007). However, large gains might be made by finding exceptional trees that do not conform to these adverse correlations. Another approach is to develop distinct breeds (or ideotypes) in which particular combinations of traits are emphasized (Carson, 1996).
- In determining heritabilities and gains the assumption is made that the population of trees for which these genetic parameters are estimated produces its seed through random interpollination, and that it has not yet undergone selection. However, this is often not so and may influence the extent of improvement that can be made.
- Site factors can influence the selection process. For example, radiata pine tends to be more malformed on fertile sites, so that selection for low malformation or sweep is easier on such sites. In contrast, the frequency of branch clusters, which is under reasonable genetic control, is less influenced by nutrition but is strongly influenced by the length of the growing season.
- The high cost involved in large-scale testing of the selected material, together with the technical expertise and support to undertake this, may cause the strategies

FIGURE 6.2

**Provenance differences: the bark on Monterey trees is thicker and more fissured than that on trees from Guadalupe Island**



Monterey provenance

Guadalupe Island provenance

employed to be modified.

- The rate of improvement made in a breeding programme is dependent on the propagation method and the time taken to obtain improved seed. The breeding methods described in the next section illustrate this.

## IMPROVEMENT OPTIONS

### Provenance selection

Exploitation of provenance variation in radiata pine has been slow, although provenance studies have been made in several countries. There can be large phenotypic differences between provenances (Table 6.2 and Figure 6.2). In Australia and New Zealand, most of the improvement has been by selection and breeding within existing land-race plantations derived from Año Nuevo and Monterey sources (Burdon, 2001). In Spain, Año Nuevo was the main source of genetic material (Aragonés *et al.*, 1997). Tree-breeders have concentrated on improving existing land-race stands because:

- There was a great deal of variability to be exploited in these stands.
- There had already been selection and adaptation towards local conditions called land races (distinctive genotypes adapted to the new habitat).
- Existing stands were thought to be derived from the better provenances.

It was fortunate that the early introductions came from the better provenances and that this gamble paid off. Furthermore, allozyme analysis has indicated that most of the variation within the two native populations (i.e. Año Nuevo and Monterey) is captured in the tree-breeding programmes. Nevertheless, it has been found that Año Nuevo provenances do better in the south of New Zealand, while Monterey is more suited to the north and on phosphorus-deficient soils (Burdon, Carson and Shelbourne, 2008).

However, provenances outside these two main areas may contain valuable traits

TABLE 6.2  
Selected provenance differences in radiata pine

Feature	Provenance				
	Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Needles per fascicle	3	3	3	2	2
Bark thickness	Thin	Thick	Medium	Very thin	Very thin
Inner corewood density (kg per m <sup>3</sup> )	325	330	320	360	360
Growth rate*	2	2	2	4	5
Frost tolerance*	1	2	4	3?	5
B deficiency tolerance*	2	2	2	4	5
P deficiency tolerance*	4	1	1	4?	5
Soil salinity tolerance*	3	2	1	5	4
<i>Dothistroma septospora</i> *	1	1	5	3	5
<i>Cylaneusma minus</i> *	2	1	5	4	4?
<i>Sphaeropsis sapinea</i> *	1	1	5	5	4
<i>Phytophthora cinnamomi</i> *	5	2	1		
<i>Peridermium harknessii</i> *	3	5	5	1	2

\*1–5 scale, with 1 = best, 3 = average and 5 = worst.  
Source: Burdon, 2001

that could be incorporated into the gene mix, or certain provenances could be advantageous on some sites (Burdon, 2001; Table 6.2). For example, the Guadalupe Island provenance has a 10 percent higher corewood density and superior straightness compared with other provenances. Although slower-growing and prone to some disease and nutritional disorders, the F1 hybrids show promise. This provenance is now being incorporated into some breeding programmes. In New Zealand, a small amount of seed is produced by control pollination, with selected mainland pollen sources applied to grafted Guadalupe plants. The importance of infusing the Cambria provenance has also been advocated (Gapare *et al.*, 2011). Cambria shows tolerance to phosphate deficiency, *Phytophthora* root rot and soil salinity, and has good stem form. However, it is more susceptible to some other diseases.

There is also interest in crossing radiata pine with *Pinus attenuata* to produce plants suitable for colder climatic conditions.

### Mass selection

Mass selection involves choosing trees based on their observable characteristics or phenotype. Some genetic improvement may be obtained by phenotypic selection of superior individuals from stands of radiata pine and the collection of their open-pollinated seed. This is a simple and inexpensive method and has the advantage that improvement is obtained rapidly for characters with high heritability. Note that under this method only one parent of the improved seed is known.

The mass selection method was used in New Zealand and Australia from the early 1960s prior to the availability of orchard-produced seed (Burdon, Carson and Shelbourne, 2008). In New Zealand, seed was generally collected from the best 25 trees per ha, either at felling (felling-select) or by climbing (climbing-select). Small but useful gains in multinodal branch habit, straightness and volume were made by this method (Table 6.3).

TABLE 6.3  
Improvement ratings for growth and form for different seedlots, New Zealand

Category	Years	Growth and form rating	GF Plus rating	Percent gain in stem volume	Percentage of acceptable stems
Unselected NZ	To 1962	1		0	45
Climbing select	1968 on	7		5–10	50
Early OP orchards*	ca 1985	14		13–18	65
Later OP orchards**	1988	16		15–20	70
CP orchards	1988	22	20–22	17–30	80
CP orchards	1995	30	23–28	20–32	80

Note: OP = open-pollinated; CP = control-pollinated; \* = selected 1950s; rogued; \*\* = selected 1968; rogued.  
Sources: Burdon and Miller, 1992; Burdon, Carson and Shelbourne, 2007; M.J. Carson (personal communication 2012 (for GMplus data))

### Advanced breeding strategies

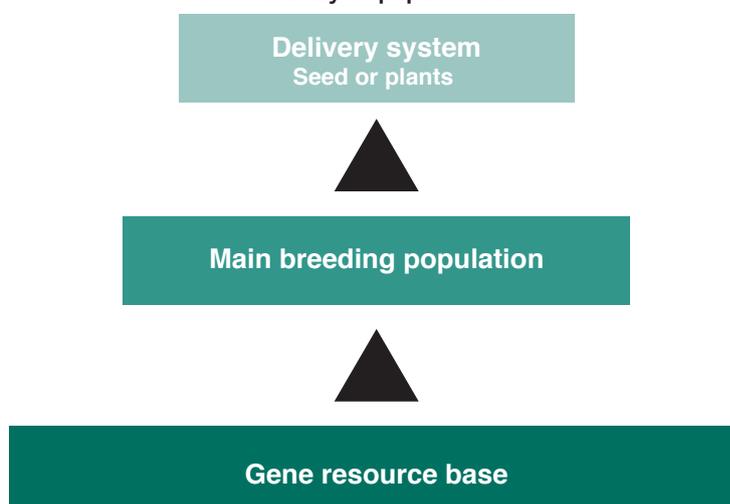
Tree-breeding strategies are devised to meet specific goals but, as discussed above, they can be difficult to define. Furthermore, goals and technology are changing (Box 6.1) and in turn influence the strategy used. Good strategies need to be flexible to allow for changes and should recognize that there is considerable uncertainty and risk. Economics must also be considered.

There are three main components to a strategy:

- organization of populations (the physical component);
- breeding methodology (non-physical design aspects);
- research component (a developmental programme feeding into both of the other two components).

A hierarchy of populations is often recognized (Libby, 1973; Figure 6.3). The base level is the gene resource, which should encompass most of the genetic variability within the species, and the gene conservation population should be managed and regenerated to ensure that a wide genetic base is maintained. For radiata pine, the gene conservation population includes provenances from California, land races and other slightly improved genotypes. The natural stands are an important part of this conservation effort, despite strict precautions on importing new material into most grower countries because of diseases such as pine pitch canker and western gall rust. Rogers (2002; 2004) studied the need for genetic conservation in California, while Gapare *et al.* (2012) reviewed and developed strategies for the *ex situ* conservation and use of these gene resources in Australasia. Fortunately, for major growers of radiata

FIGURE 6.3  
The hierarchy of populations



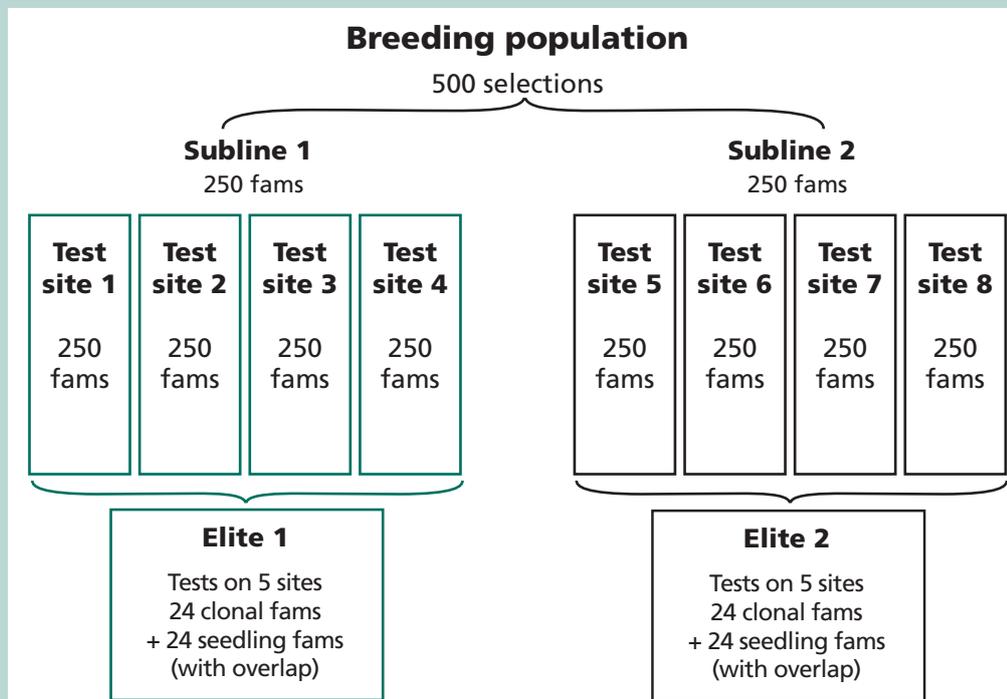
pine, a series of collections was made from the natural stands in California, with a major seed collection in 1978 that is known as the Eldridge collection (Burdon, Carson and Shelbourne, 2008; Gapare *et al.*, 2012). The seed from these stands has been planted at more than 100 sites, mainly in Australasia, including in specific gene resource plantings, and there are plans to ensure that more conservation plantings will be rolled out over time. Seed and pollen are also being kept in long-term storage. This base population can be drawn on to introduce further genetic variability into the breeding programme and perhaps to introduce new characters that are poorly represented in the current breeding population. It may also be viewed as part of the genetic defence against potential threats such as disease.

The breeding population, drawn from the base population, usually has 300–500 parents at any one time. Current plans, for example, suggest there will be 500 parents in the breeding populations of the joint “New Zealand plus New South Wales” breeding programme (Dungey *et al.*, 2009) (see Box 6.2). The Southern Tree Breeding

## BOX 6.2

### Structure of the joint New Zealand plus New South Wales radiata pine breeding programme

The most recent breeding strategy for radiata pine in New Zealand and New South Wales, Australia, is based on 500 selections which will include the infusion of ten selections from less-represented provenances. This breeding population is subdivided into two independent sublimes, each with 250 families (fams). The progeny of these selections will each be tested on four sites, for a total of eight test sites.



On the basis of these progeny tests, an elite group will be selected for each subline. Each elite group will have 24 control-pollinated clonal and 24 seedling families that may overlap and will be tested on five sites. If needed, the sublimes or elite groups could be crossed to overcome any inbreeding. Source: Dungey *et al.*, 2009.

Association, based in South Australia, has 340 parents. In the small radiata breeding programme in Galicia, Spain, over 50 trees were selected and have been used in a seed orchard and in progeny tests (Codesido and Fernández-López, 2009).

The breeding population can be divided into sublines representing replicate breeding populations that can, if needed, be crossed to ensure completely outbred offspring (i.e. offspring that are unrelated). This concept has been incorporated into the joint New Zealand plus New South Wales breeding programme, as well as the plans of the Southern Tree Breeding Association (Box 6.2). The Southern Tree Breeding Association is moving from discrete generations of breeding towards a dynamic rolling front, since this will lead to increased gains and efficiencies (Wu *et al.*, 2007). The joint New Zealand plus New South Wales programme keeps discrete generations at the subline level and has a rolling front approach for the elite population (Dungey *et al.*, 2009).

There may be several smaller trait-based subpopulations within each subline to produce specific breeds. In recent years, the New Zealand programme has produced three distinct breeds: a growth and form breed, a long-internode breed for clear-cuttings, and a breed for structural timber (Burdon, Carson and Shelbourne, 2008). At one stage there was a dothistroma-resistant breed, but this is now part of the general breeding programme, along with breeding for resistance to *Cyclaneusma* needle cast. The recent strategy for the joint New Zealand plus New South Wales breeding programme calls for a general elite population within each subline that will test the performance of both control-pollinated clones and seedlings, on a rolling front approach (Dungey *et al.*, 2009; Box 6.2). The Southern Tree Breeding Association has three breeds: multi-purpose, density and growth, and *Phytophthora* resistance (Wu *et al.*, 2007).

At the top of this hierarchy is the seed-producing or plant-producing population (Figure 6.3). Parents in this population have been selected from the breeding population to form the basis of the seed orchard, or for using other techniques to produce improved planting stock.

The early tree-breeding programmes employed open-pollinated seed orchards using grafts of selected parents (Burdon, Carson and Shelbourne, 2008). Later, on the basis of progeny tests, the worst parents were removed, or new orchards were established on the basis of proven general combining ability. Grafting incompatibility, site limitations and external pollen contamination were often problems with these orchards. These “classical” seed orchards provided large quantities of modestly improved seed (Table 6.3). Open-pollinated seed orchards currently provide about half of the radiata pine seed used in New Zealand, although today the grafted trees are hedged to make it easier to collect cones. The new hedged open-pollinated seed orchards are spaced at 4 m x 2 m and are expected to have a life span of up to 20 years (S. van Ballekom, personal communication, 2012).

The control-pollinated orchard concept was developed in the 1990s. It adopted closer spacing and grafted trees that were maintained in hedged form, enabling operators to carry out controlled pollination at near ground level (Carson, 1986; Burdon, Carson and Shelbourne, 2008). At the Amberley seed orchard in New Zealand, the current practice is to establish twin rows at 1 m x 1.5 m spacing along the rows and a 4 m-wide strip between the twin rows (Figure 6.4; S. van Ballekom, personal communication, 2012). This enables easy access to the grafted plants and assists with orchard maintenance. Flowering is stimulated using gibberellin injections, and dry pollen is applied to the bagged female strobili when they become receptive. In New Zealand, the best seed orchards are close to the sea in areas of high sunshine and low rainfall. Control-pollinated orchards almost double the genetic gain in the progeny compared to open-pollinated orchards but triple the cost of producing seed. Large breeding archives have been established in New Zealand and the application

FIGURE 6.4  
Control-pollinated seed orchards at Amberley, New Zealand.



S. van Ballekom

Note: twin rows of trees

of similar procedures to these archive trees is enabling shorter turnover of breeding generations, leading to the prospect of faster genetic gains.

The parallel development of mass production by nursery cuttings, micropropagation and, more recently, somatic embryogenesis (see Chapter 7) has provided new avenues for obtaining planting stock from this greatly improved seed. It is now possible to deploy selected clones to achieve even larger gains and to customize seedlots, clonal mixes and single clonal varieties commercially for specific growers and sites (Carson and Carson, 2011). Current commercial varieties of radiata pine available in New Zealand and Australia show increases of about 25 percent in volume and dry matter production and 30–60 kg per m<sup>3</sup> in basic wood density compared with open-pollinated and control-pollinated seed orchard stock. They also have improved wood stiffness (Figure 6.1).

Other options for deployment have also been suggested (Dungey *et al.*, 2009), such as converting advanced progeny tests into seedling seed orchards after removing less-desirable individuals.

### Incorporation of desired traits

The importance of selecting breeding goals, and thus the traits for improvement, has already been stressed. In practice, conflicts may arise over which traits are more important, and methods are also needed to incorporate and evaluate the use of multiple traits.

Selecting traits in tandem (i.e. sequentially, one at a time) has not proved applicable to radiata pine because of the long breeding cycle. However, it can have advantages where traits vary widely in either cost of assessment, optimal age of assessment, or where there are adverse genetic correlations between traits. The use of independent culling levels has also not found general favour, although it has been used to remove breeding parents that are particularly susceptible to a given disease. Tree-breeders have largely used selection indices.

The selection index combines the weights and scores for traits according to economic and genetic data for a candidate tree as well as its family. This method is used by all the main radiata pine growers. The main problems have been:

- determining economic weights, which could change with time or industrial end user;
- variability in the age at which traits can be evaluated (for some, such as growth rates, the older the tree the better);
- adverse genetic correlations, such as, for example, between growth rate and wood density.

Although there have been substantial developments in recent years, the task of incorporating desired traits remains challenging (Burdon, 2008; Burdon, Carson and Shelbourne, 2008; Wu *et al.*, 2007).

### Other recent developments

Other developments being actively pursued in radiata pine breeding include the following:

- Techniques have been developed to screen for stiffness and shrinkage in the corewood of radiata pine in trees less than two years of age (Apiolaza, Chauhan and Walker, 2011). This may provide an additional strategy for reducing the problems of poor-quality corewood in radiata pine (see chapters 5 and 9).
- Information management systems are being improved to enable access to data on over 500 000 trees in Australasian radiata pine breeding programmes. New data are continually being generated.
- New statistical tools are enabling improved estimates of breeding values.
- The use of gene markers for identifying quantitative traits is a promising approach to characterizing trees that may allow better selection using fewer progeny trials. They may also help to minimize inbreeding.
- The development of designer trees is a possibility and could lead to greater domestication of radiata pine and enhanced profitability (Carson, 1996; Carson and Carson, 2011).

### DOMESTICATION PROGRESS

The native radiata pine stands have evolved in different directions as they adapted to specific sites after becoming isolated from one another. Similarly, the species has adapted rapidly to local conditions when planted in other countries, leading to the creation of local landraces over a period of about 50 years. The finding of induced resistance for pitch pine canker is intriguing and illustrates how radiata pine trees can perhaps adapt to new stresses without going through a sexual phase (see Box 4.2).

Tree-breeders and forest managers have altered the slow natural selection process in order to meet industrial needs. Over the last 60 years, tree-breeders have increased stand productivity and the stem straightness of trees developed from seed provided to growers (Table 6.3). The data presented in Table 6.3 hide the fact that trial results show that average growth rates differ with site and are greater on high-quality sites, and that percentage gains can decrease slightly during the crop rotation (Burdon, Carson and Shelbourne, 2008). Further, as Figure 6.1 and Box 6.1 illustrate, there are considerable additional gains to be made using clones. However, there have been some unintended changes with these breeding programmes, including reductions in wood density and perhaps increased susceptibility to magnesium and insect stresses (Beets *et al.*, 2004; Sorrenson, 2007; Kay, 2008). Burdon (2008) argued that the species is still in the early stages of domestication compared with agricultural crops. He suggested that the use of new vegetative propagation systems, integrating breeding with molecular biology and genetic engineering, to design trees that produce a greater amount of high-quality wood could lead to the further domestication of the species.

Improved silvicultural practices also affect the growth of stands, with the magnitude of gains depending on the limiting factors that are being overcome (Mead, 2005a; see Chapter 10). For example, very large responses are possible from the application of fertilizers to infertile soils, by improving soil rooting depth and through woody-weed control. For particular sites, all these can increase productivity as much as or more than has been achieved by tree-breeding. However, tree-breeding promises further gains with additional research efforts. Overall, doubling the productivity of wild Californian stands is possible in radiata pine plantations (see Chapter 10). This and more has already been achieved in some eucalypt plantations (Mead, 2005a). The domestication of rubber (*Hevea brasiliensis*) increased latex production by 8–10 times, of which 70–80 percent resulted from breeding and the selection of clones and the remainder from husbandry (Webster and Baulkwill, 1989). The success of rubber was also based on a large genetic x husbandry component – to get very high yields, both good clones and good husbandry are required. The integration of tree-breeding with other silviculture practices will also be critical for the full domestication of radiata pine.