Chapter 5
Development of the Management Concept While Tree Improvement Shifts Gears: 1969–1983

5.1 Introduction

In 1967, Australia had just made its first operational collections of seed-orchard seeds, and such a collection was made a year later in New Zealand. The year 1968 also began a new era for breeding radiata in New Zealand, with the selection afresh of vastly more plus trees from New Zealand land-race plantations. This latter advance was based on Gene Namkoong's contributions to breeding theory appropriate for forest trees, and Tony Shelbourne's strategic planning and implementation of that theory focused on radiata in New Zealand. The resulting update of the breeding strategy greatly increased the numbers of plus trees, and thence the scope for reselecting outstanding parents on progeny performance. That also increased the available genetic diversity in the New Zealand base breeding population.

At about the same time, important developments were taking place on other fronts, making the late 1960s even more important as radiata domestication accelerated. Within New Zealand, radical new silvicultural regimes were being developed, and soon were implemented. The so-called "Direct Sawlog" (or "Direct") regime included much wider initial spacing at planting, earlier thinning to remove the apparently poorer trees and achieve even wider spacing, and aggressive pruning, all focused on more quickly producing larger and more-valuable final-crop trees. This early selection and spacing of the crop trees, plus pruning boles to about six metres height, was meant to achieve larger, higher-quality butt logs, while genetic improvement was counted on to defend the quality and value of unpruned upper logs. Nursery and field establishment practices were soon to be revolutionised (Maclaren 1993; Mead 2013), which had the additional benefit of allowing much better yields of planting stock from the scarce, genetically improved seed coming from the early seed orchards.

Also occurring in New Zealand, a National Development Conference was held in 1969; it endorsed the view that New Zealand needed a major expansion of its plantation forestry estate (Fig. 3.1), both for profit and for broadening the

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country's narrow base of export products, and that became part of government policy (Roche 1990). This roughly coincided with the lifting of price controls on sawn timber which had encouraged profligate use of the fast-dwindling native timber resource. In Australia, at about the same time (from 1966), central government had been persuaded to encourage new forest plantings to reduce dependence on imported softwood products (Johnson et al. 2008; Bevege 2010). In both countries, expansion of plantation forests thereby became much more active during the next few years. In several Australian states the new plantings were increasingly being concentrated on sites where previous experience indicated radiata would do well, often leading to the clearing of eucalypt forest for the plantations. Such clearing of native forest led to community opposition (e.g. Routley and Routley, 1975), and in the 1980s in Victoria, for example, such clearing was phased out (Lavery 1988) and new plantings to expand the forest estate were mostly on former farmland. Fertility on these former farming sites had often been built up through pastoral practices such as the cultivation of legumes and the addition of superphosphate. By the 1980s this factor, together with increased application of fertilisers (e.g. Boardman 1988), better weed control and a trend to lower stocking and shorter rotations (e.g. Lavery 1988) combined to present cultural environments often biologically and physically very different from those in which the first-generation seed-orchard trees had been selected.

In Chile, major developments in radiata breeding, silviculture and plantation management came later, and involved both institutions and policies. After the military coup of 1973, central government renewed vigorous promotion of new forest planting, mindful of the country's extreme dependence on copper exports. Breeding of radiata began in the 1970s, and greatly benefitted from hard-won experience in New Zealand, at the time freely shared by FRI. Large processing plants were established in Chile during the early 1970s, with a heavy emphasis on pulping, to deal with the big resources of Chilean radiata wood becoming available. By comparison, such industrial developments were modest in Australia, New Zealand and South Africa.

Many important developments leading to more-intensive breeding of radiata in Australia and New Zealand followed increased support by central governments for radiata breeding in those countries. Operationally, those breeding programmes had by 1983 advanced into second-generation selections among partially-pedigreed offspring of the early plus-tree selections and progeny tests. Also, by 1983 the outturn from New Zealand's seed orchards was close to meeting the entire national planting requirements, which it did in 1986. However, progress towards that goal was abruptly checked in South Australia by disastrous fires early in 1983, which consumed not only some seed orchards but also major stocks of seed in storage. The resulting shortfall was greatly exacerbated by the urgent need to restock large areas of burned forest. Some four million seedlings, supplemented by half a million rooted cuttings from orchard seed, were raised per annum, resulting in the largest use of vegetatively-propagated radiata to that time.

By the mid-1970s, the quantitative genetic architecture of radiata was becoming much better known, for a wide range of traits. Variation among provenances was much better characterized, and information on several genetic parameters, notably heritabilities and genetic correlations, was increasingly solid. The new information on provenance variation prompted further larger collections of seeds from all five native populations in 1978, in order to boost available genetic resources. The collecting expeditions were sponsored and staffed by Australia and New Zealand, with additional financial support from the US National Science Foundation and important local collaborations in Mexico and California (Eldridge 1978). Besides making additional founder collections of native seeds, the participants added to previous observations of the character and condition of the native radiata pines. Among those observations was a reminder that the open-grown pines on Guadalupe Island, while exposed to repeated gale-force winds, had remarkably straight boles, unlike similarly exposed mainland radiata pines.

Moving beyond the first generation of intensive breeding provided much of the context for developing tree-breeding strategy worldwide, as a discipline in its own right. Breeding strategies were advanced while addressing several issues of propagation and silviculture of radiata, presented in detail later.

Importantly, constructing a more robust breeding strategy classically involved a hierarchical organization of breeding material (Libby 1973): from top-ranked material for immediate commercial deployment, underpinned the breeding population in which intensive genetic gain was pursued over successive generations, which in turn are underpinned by genetically-diverse collections of land-race and native-population base samples at the lowest level of the hierarchy. Controlled pollination among parents in appropriate mating designs was another key plank of the evolving strategies. Underpinning the developments in breeding strategy were developments in quantitative breeding methodology (Burdon et al. 2008).

Better field experimental designs were generally being adopted, often to accommodate greatly enlarged breeding populations and the large areas of ground needed for genetic tests of candidate trees. Selection procedures were made more objective and efficient, with improved laboratory and field assays of wood properties, and computer-based statistical analyses of the floods of data being generated. Furthermore, analyses of genotype-by-site interactions were developed and included in setting tree-breeding goals and implementing strategies during the time period of this chapter.

Much effort was devoted to improving breeding technology. Controlled-pollination techniques were improved (Burdon et al. 2008). Despite seed orchards eventually delivering genetically improved seeds, various problems with seed orchards became clearer, and were vigorously researched. In the course of seed-orchard research, new technologies were developed for rooting cuttings taken from grafts of mature trees that were at risk of delayed graft incompatibility. Such cuttings were then used in seed orchards.

Technology for vegetative propagation has applications well beyond breeding technology, since mass-production of cuttings from pilot quantities of genetically elite seed is a means of quickly and massively delivering genetic improvements in growing stock. Indeed, acquiring cuttings from serial propagation of young seedlings and/or from juvenile hedges (Libby et al. 1972) was being developed for such mass-propagation, while the foundations were laid for future production of **plantlets**^{G} by *in-vitro* tissue culture.

The need arose to demonstrate and quantify genetic improvements, partly for political purposes to secure industry support and continued or increased funding, and partly for better projections of future forest yields and log characteristics. For all this, better information than then available was needed. It had been assumed that comparing the genetically improved trees with unimproved "control" trees in properly replicated progeny trials would suffice, but questions were raised as to how much improvement would be expressed in operational plantations where differences between select and control material would not be amplified by competition effects. The impetus for better information first came in Australia, where J.D. Ovington of the Australian National University had queried the scale of genetic gain likely from breeding programs. New Zealand followed soon after, establishing a network of genetic-gain comparison trials (Sect. 5.5.7) on a range of sites, the first of which were planted in 1978. Progress was subsequently made in modelling performance, towards harvest age, of the genetically improved stock (Carson et al. 1999).

Meanwhile, well before 1983, the understanding of where radiata could be grown successfully had advanced, and we next review (Sect. 5.2) that enhanced understanding. Moreover, the improvements in nursery, field-establishment and management practices were continuing to extend the range of sites where radiata could be grown successfully (Sect. 5.4.2).

On the global scene, Australia hosted at Canberra the Third World Consultation on Forest Tree Breeding, under the auspices of FAO and IUFRO (International Union of Forest Research Organisations). Breeding radiata featured prominently in the proceedings, and a IUFRO Working Party on Breeding Radiata Pine became reactivated as a vehicle for exchanging information and ideas.

5.2 Where Which Species Will Perform Well

It was good to learn the range of sites and conditions where radiata would grow well. It was even better to learn where it would remain preferred over other valuable species that could also grow well there. The earlier, often informal species-introduction trials, current and predicted markets, and desires for some diversification, drove decisions to plant radiata and/or some alternative species. Between 1951 and the 1970s, the picture of all the then-contesting species' site tolerances changed, largely through the advent of some fungal pathogens, but partly through developments in management practice for radiata (Sect. 5.4). It was found that, relative to such attractive alternatives as some acacias, Douglas-fir, some eucalypts, some various other pines, and coast redwood, radiata was usually preferred in Chile and New Zealand. Radiata was widely preferred in south-eastern Australia but less so farther west and north. In South Africa, Spain and some other Mediterranean countries (Italy, Albania, Greece and Turkey) climates were locally congenial but suitable soils were often even more localised. In California itself, sites that permitted rapid tree growth and good health in radiata proved very localized.

An alarming biotic event had been the spread of the needle-cast pathogen *Dothistroma pini*. Known earlier only as a nuisance pathogen in Christmas-tree growing in USA, it spread to many parts of the world during the late 1950s and the 1960s (Gibson 1972). It effectively eliminated radiata as a species option on many high-altitude sites in East Africa and Hawaii where it had previously grown well (Burdon 2001). In New Zealand there were large areas where the future of radiata came into question. A multi-pronged genetic response included: collecting and stockpiling large amounts of seed of *Pinus patula* (Mexican weeping pine) which was known to be resistant, attempting to cross radiata with *P. patula*, selecting and cloning healthy radiata pines growing among heavily infected neighbours, and importing radiata clones selected for resistance in Kenya. However, the immediate practical solution lay in FRI developing an effective and quite cheap protocol for aerial spraying with copper compounds that controlled the disease (Kininmonth 1997b; Mead 2013). Because radiata's susceptibility typically gave way to effective "ontogenetic" resistance before about age 15 years, such protective spraying could usually be discontinued after only two or three applications. This solution for those plantations at risk maintained confidence in the species among growers. Ironically, after the initial scare, radiata became the preferred species in New Zealand more than ever, because other pines (particularly Corsican and ponderosa) that had been planted widely remained highly susceptible even as mature trees. After appearing in both Australia and Chile, dothistroma was not perceived there as such a big threat, because severe disease was much more localized and did not significantly affect radiata in its most important plantation-growing areas.

Decisive advances in management inputs occurred in both establishment practice and use of fertilizers. Producing more-vigorous and better-conditioned nursery stock, in conjunction with better site-preparation practice, allowed radiata to be grown over large areas in New Zealand that were subject to severe ground-level frosts and had previously been planted with more-frost-hardy pines. Nutrient deficiencies had been recognised at a range of sites in Australia in the 1930s; applications of zinc and phosphorus produced strong responses on sites where these elements were limiting factors (e.g. Stoate 1950). By the 1980s, nutritional constraints and opportunities for benefits—especially those involving nitrogen—on the old soils typical of Australia were much better understood (Australian Forestry Council 1981).

In New Zealand correction of phosphorus deficiency had been developed during the 1950s (Weston 1956, 1962). The existence of an agricultural aviation industry topdressing hill-country pastures with superphosphate made application to forestry straightforward. As a result, radiata could thus be grown over a much larger area in the far north of the country, and plantings there were a significant component of accelerated new planting from the early 1970s. Also in New Zealand, boron deficiency as a cause of shoot dieback and consequent stem malformation was recognized as a local problem (Stone and Will 1965), but correction by application of boron was usually straightforward. Often, however, the practical limits for growing radiata commercially in New Zealand were and are set by the terrain rather than by climate, soil fertility and/or distance to ports or local markets.

In Chile, multiple nutrient deficiencies were evident in radiata on the degraded Coast Range soils that had been widely afforested. In addition, boron deficiency symptoms were often severe on radiata pines planted in weathered granite or river-borne volcanic ash, causing much bole malformation (Schlatter and Gerding 1985). These nutrient deficiencies seldom prevented people from planting and growing radiata on such soils, but more prompt correction of known deficiencies would often have greatly improved the value of their harvested trees.

In South Africa, radiata plantations, after some ambitious and ill-fated siting, became confined almost entirely to a strip with winter-rainfall climates near the south coast extending westwards from slightly east of George. However, until widespread phosphorus deficiency was recognised as affecting radiata (Donald and Glen 1974; Donald et al. 1987), maritime pine was preferred for the less fertile sites in this zone.

In Spain, new planting continued along the north coast, mainly near the western end of the Pyrenees in the Basque Country. Despite frost-kill of some 20,000 ha of radiata plantation in the province of Guipuzcoa (E of Lat. 2°W) in 1956, new planting had accelerated sharply from around 1954 till 1973, by when the area of radiata in the region had increased from around 60,000 to 160,000 ha (Michel 2006).

Near the Equator in South America (Ecuador and Colombia) considerable plantings of radiata have since been made (P.G. Cannon, pers. comm. to RDB 1993), presumably using seed from Chile. While radiata does tolerably on these high-elevation sites (Miller 1974), interestingly, as of the end of the 20th century, several provenances of the related bishop (muricata) pine were looking better (pers. obs. WJL in 2001).

Geographic ranges of radiata plantations in the main grower countries are summarised in Table 5.1.

Table 5.1 Approximate latitudinal and altitudinal ranges of main areas of radiata plantations, by country (After Burdon 2001)

Country	Latitude (°)	Location	Altitude (m a.s.l.)
New Zealand	34½*–46½	North	0–700
		Far south	0–300
Chile	35–40		0–800
Australia	33–43½*	New South Wales	400–1,100
		W. Australia	0–300*
		Victoria & S. Australia	0–700
		Tasmania	0–400
Spain	42½–43½*		0–400
South Africa	33–35*		0–1,000

*Range limited by extent of landmass or lack of elevated topography

5.3 Institutional Developments

During 1969 to 1983, actual institutional changes in Australia, New Zealand and South Africa were generally modest, although important developments occurred affecting the growing of radiata. Institutional changes in Chile, however, were dramatic, with political turmoil followed by a military coup with its bloody aftermath. For the forestry sector, along with the rest of the country, it was a turbulent period, but in the latter half there were important developments in the growing, utilization and breeding of radiata.

5.3.1 Australia

The rate of new planting of radiata in Australia, with government support, increased markedly during the period (Table 5.2). This challenged breeders and seed-orchard managers to supply more genetically-improved seed. In view of the lead time needed to increase supply, the seed orchards coped well with the challenge. Moreover, by the end of 1982 it was shown to be operationally practicable to greatly extend an inadequate supply of high-quality seeds by taking and rooting cuttings from young seedlings.

In addition to these public-sector activities, planting by private-sector corporate entities was significant in these years (Table 5.3). The largest areas of private radiata pine plantations were in Victoria, New South Wales and Tasmania. In eastern Victoria, APM Forests had an active seed-orchard programme. Two other private-sector entities participated in efforts to improve the genetic quality of radiata: Saxton's in Gippsland—who developed and operated a seed orchard—and Francis Clark in NSW who (not far from Canberra) propagated and sold rooted cuttings of selected families he acquired from the CSIRO breeding programme. Saxton's orchard was eventually to come under the management of Seed Energy using genetic material under licence from the Southern Tree Breeding Association (STBA; see below).

Table 5.2 New areas of radiata planted annually in Australia (ha)*

Year	Forest service							Private	Total
	NSW	Victoria	Queensland	South Australia	Western Australia	Tasmania	ACT		
1965	3,400	2,200	60	2,110	500	730	0	2,350	11,350
1968	6,040	4,610	100	2,710	800	1,760	210	..	16,230
1969	8,310	2,450	110	2,410	430	1,880	100	..	15,690
1983	5,320	2,070	0	1,890	1,380	900	0	12,400 (1982)	23,960

*These figures, derived mainly from annual reports, are indicative because a few of the smaller numbers include replanting of small felled or burnt areas, and the reported timing of inventories within calendar years was not consistent

.. = not available

Table 5.3 New areas of conifer plantations established in 1975 in Australia (ha)*

Sector	State or territory							Total
	NSW	Victoria	Queensland	South Australia	Western Australia	Tasmania	ACT	
Private	1,837	5,175	625	515	900	1,687	0	10,739
Public	7,143	4,297	5,457	3,042	2,218	1,795	553	24,505
Total	8,980	9,472	6,082	3,557	3,118	3,482	553	35,244

*See footnote to Table 5.2. Also, most of this planting was of radiata; the exceptions were in Queensland (where almost all was other species) and in Western Australia (where about one-third was radiata)

The first meeting of the Australian Forestry Council's Research Working Group No. 1, Forest Genetics, took place in 1967, and subsequent meetings were held at intervals of two to three years, usually with observers from New Zealand. (Other working groups, for example Soils and Nutrition, concurrently became active and contributed to the improved management of radiata plantations). Information and genetic material (mostly plus-tree pollen and scions) was shared among members, and opportunities to further this cooperation were explored through a sub-set of group members. As the period drew to a close, extensive but unstructured collaboration that had evolved culminated (in 1982) in the formation of the Southern Tree Breeding Association. Based in Mt Gambier, the STBA was an "incorporated non-profit organization funded by industry in the "Green Triangle" region of south-eastern SA and western Victoria"; it "was established with the assistance of CSIRO for two companies [Softwood Holdings Ltd and Sapfor] [growing radiata] and the state government of SA." This move was intended to mitigate some organizational difficulties and permitted some economies of scale, but could not eliminate the downsides of geographic and organisational dispersal of the national breeding effort with radiata. Straddling state borders as it did, the STBA was a major development that later became a national organisation serving about half the radiata estate and breeding of species additional to radiata (Wu et al. 2007; http://www.stba.com.au/page/home). Among its first responsibilities under David Boomsma was the management of the seed orchards established by the South Australian Woods and Forests Department.

In 1975 the Australian federal government transferred the Forest Research Institute of the Forestry and Timber Bureau to the Commonwealth Scientific and Industrial Research Organisation (CSIRO), paving the way for the appointment of additional specialist staff in Canberra and Mt Gambier to undertake research and development related to forest genetics and tree breeding.

The appointment of J.J. Landsberg in 1981 as the second Chief of the CSIRO Division of Forest Research led to a surge in ecophysiological research on radiata; close collaboration later followed with New Zealand tree physiologists led by David Rook. An important outcome of this work was the development of growth models that drew together a wide range of research results on water availability, nutrition, stand conditions and other environmental factors (e.g. Landsberg et al. 1988).

5.3.2 New Zealand

In New Zealand, the main institutional development during this period was the commitment of Tasman Forestry Ltd (Tasman) to radiata breeding, led by John Gleed, who had been their nurseryman. The company established its own seed orchard, using parents selected by FRI and then progeny-tested by FRI near Tasman plantations. Located on a warm, low-altitude site subject to sea breezes, that orchard produced seeds relatively quickly and in abundance.

The then-biggest private forestry company, NZ Forest Products Ltd (NZFP), made substantial forays into its own tree-breeding and seed-orchard development, specific to their lands and goals. Compared with the Tasman initiatives under Gleed, however, NZFP commitments were inconsistent, and were thus without lasting impact either in advancing their own local radiata breeds or on public and professional recognition for producing genetic information.

FRI remained overwhelmingly the dominant player with respect to radiata's domestication in New Zealand, and perhaps the world. Besides continually improving understanding of radiata's potential on various New Zealand sites, and of how broadly given families or clones could be deployed over a range of contrasting sites, FRI aggressively continued genetics research, practical breeding, and trying various management practices.

In 1970, FRI hosted a second Symposium on Pruning and Thinning Practice (James et al. 1970; Sutton 1970), its first symposium on these topics having been held in 1963. This second symposium soon proved far more influential in respect of silvicultural regimes. For genetic improvement, one of the papers (Shelbourne 1970) importantly foreshadowed the concept of radiata breeds and clones differentiated on technical properties of the trees and likely end-products rather than on regional adaptation (Sect. 5.5.2). Later, FRI hosted two International Union of Forest Research Organizations (IUFRO) meetings, one in 1973 on Vegetative Propagation (mainly focused on radiata) and the other, in 1982, on Breeding Radiata Pine. These latter two meetings both produced and synthesised ideas and data on breeding and management of radiata, thus supporting and progressing the early domestication of radiata both locally and worldwide.

In 1970, a largely-personal initiative was conceived and launched by the NC-State-trained geneticist Tony Shelbourne of FRI. He induced geneticists and tree breeders in Australia, France, Kenya, New Zealand, South Africa and the US to contribute select radiata material (largely as single-parent open-pollinated (OP) progenies from seed orchards) for a series of International Gene Pool trials. Within Australia, eight breeding programmes contributed seeds of their plus-tree lines, and the US added some OP families from apparent plus trees in the five native populations. Research plantings were made in five countries, although only three of those countries (Australia, New Zealand and South Africa) produced reported results (Burdon et al. 1997). Some of the findings indicated where parents could be selected or tested effectively for what sets of sites; this involved how well progeny differences were resolved on the various sites and how consistent progeny rankings were between pairs of sites, which is valuable information. However, the project was conceived primarily to share valuable breeding material among programmes in different countries. Many selections were later made from these trials for incorporation in local breeding programmes.

In 1982 a new Propagation and Early Growth (PEG) research unit was created at FRI, which was separate from the Genetics and Tree Improvement (GTI) unit. This removed responsibility for more-effective propagation from geneticists and breeders. While it led to some communication gaps, it helped bring to better enlist the expertise of tree physiologists and nursery research personnel.

5.3.3 South Africa

The national Department of Forestry, which had initiated radiata breeding in the early 1960s, became in 1980 the Directorate of Forestry within the newly created Department of Water Affairs, Forestry and Environmental Affairs. While the Directorate retained responsibility for operational breeding of radiata, which it ran from Saasveld, Stellenbosch University over time became increasingly involved in silvicultural research on this species.

5.3.4 Chile

Purposeful tree breeding started much later in Chile than in Australia, New Zealand and South Africa, despite the large size of Chile's plantation estate of radiata. In the early 1970s, plus trees were intensively selected under the direction of Norman Smith, a Chilean forester of Instituto Forestal, the central government's forest research organization. Seeds were collected from these trees and extracted, but the fledgling breeding programme fell victim to political upheaval leading up to and following the military coup in 1973 and the subsequent exodus of almost all of Instituto Forestal staff. While some experienced staff were laid off or redeployed, many moved pre-emptively into other employment. Later, in 1978, some plus trees that had been chosen by Norman Smith could be relocated, but the seed that had originally been collected from all of them was mixed together before sowing in the nursery, precluding any effective progeny testing.

During this period, the University of Chile became involved in research on genetics of radiata, and that research also met with disasters resulting directly from political upheaval. During the unrest leading up to the military coup, Jochen Kummerow, a professor at the university, was raising seedlings in a greenhouse from seed provided by Libby from the five native-provenance native populations for replicating provenance-progeny trials in the US, New Zealand and Australia. Kummerow got beaten up by striking students, and the seedlings perished from lack of watering while he was recovering in hospital. Martin Bannister from New Zealand's FRI visited the university during the unrest in 1973. With Dr Harald

Schmidt as his host, they collected cones from vigorous well-formed trees in a large number of Chilean radiata plantations, intending to share the seeds between Chile and New Zealand. While such seeds would have been of great value for research and breeding, they just disappeared during the turmoil.

Well before the political upheavals, moves had been made by the Chilean government to develop manufacturing industries to process wood from the radiata plantations. FAO personnel had been active in Chile from the mid-1950s (Scott 1960) in surveying the young radiata resource with the intention of guiding the establishment of strategically located pulpmills. Even so, one big Chilean-owned company, CMPC, had already set up its own industrial plant, dominated by a kraft pulpmill that had opened on a modest scale in 1959, while a smaller company had established a **hardboard**$^{\mathbf{G}}$ mill. However, there were large areas of radiata plantation, in varyingly fragmented ownership, for which no provision had been made to process harvested wood. There was much consolidation of forest ownership, which then facilitated the supply of wood for the mills. Despite the disruptions caused by political upheavals and much nationalization of forests and businesses, three pulpmills were established by 1977. Sawmills had been established, but on nowhere near the scale needed to deal with the increasing volume of wood that was becoming available for harvest.

After the military coup in 1973, the new government soon vigorously renewed strong financial encouragement of additional afforestation. This was prompted by a combination of factors: a desire to diversity Chile’s export markets from the extreme exposure to the copper market; an appreciation of the comparative advantages of growing wood on the lower-quality land; a response to high unemployment; and a need to rehabilitate large areas of badly-degraded farmland. (Ironically, this was massive state assistance on the part of a right-wing government that a few years later was true to its political colours with vigorous privatization.) In response, planting rates boomed, and radiata was chosen for most of the plantations. Genetic improvement of radiata resumed within a new institutional structure that was founded in 1976. It followed the pioneering 1960s model of the North Carolina State University (NCSU) /Industry Tree Improvement Cooperative that was operating with loblolly pine, but was called a “Convenio” (“agreement”) because “Cooperativa” (“cooperative”) was seen by the right-wing military government as socialist. The model was set up with the advice from Bruce Zobel, Director of the NCSU Cooperative. The founding Director of the Convenio was Roberto Delmastro, a former graduate student of Zobel’s and a faculty member of the Forestry School of Universidad Austral de Chile at Valdivia.

In the Convenio, each member company agreed to have its own clonal seed orchard, with the Chilean forest service (CONAF, the Corporación Nacional Forestal) operating as a member sponsoring two of the orchards. Compared with the NCSU Cooperative, the membership of the Convenio was more heterogeneous. Members of the former were typically vertically integrated companies, growing much of the wood that they processed, with individual company sizes largely governed by the economies of scale of kraft pulpmills. In the Convenio, the sizes of companies and the nature of their operations were more varied.

In 1978, Rowland Burdon, after 14 years' experience in New Zealand's FRI, served for two months as FAO Consultant to the Convenio (Burdon 1978), checking plus-tree selection, propagation practice and orchard siting, and then reviewing the overall direction of the programme. Significantly, much had been learned from the early and often bad New Zealand and Australian experiences of orchard siting, and Convenio members thus avoided repeating some of those early mistakes. The concept of the breeding cooperative entailed each member company assuming operational responsibility for its own breeding programme, with technical guidance from Director Delmastro at Universidad Austral. The two CONAF orchards were established to provide seeds to serve forest owners outside the Convenio. Advantages included a sense of ownership of their own breeding programmes and spurring of competition among the companies. The emphasis on individual ownership, however, did lead to a lack of national coordination in managing the genetic material.

Following up on Burdon's visit, a party of six personnel from within the Chilean Convenio, mostly young tree breeders, was sent on a short tour to New Zealand by FAO in 1979.

With the prospect of intensive genetic improvement and with increasing technical contact with New Zealand, other aspects of growing radiata began to change in Chile. Nursery practice there had been driven by considerations of cost and the pious belief that first-year survival after planting was a sufficient measure of planting success. Yet with the genetic improvement yielding initially limited amounts of very valuable seed, obtaining more and better-quality planting stock from the available seed became very attractive.

Thinning and pruning in Chile had usually been minimal at best, and typically low rates of natural mortality from inter-stem competition (despite radiata's good assertion of crown dominance) meant that thinning in order to harvest stems before they died was not a pressing issue. Nevertheless, interest increased in active tending to improve economic returns. Various study tours and consultancies continued between New Zealand and Chile through 1983 and beyond.

5.4 The Context of Intensifying Management Practices

5.4.1 Introduction

For radiata, we have addressed in Chap. 4 early work on the second of the two main planks of domestication, namely genetic improvement. The early development of the first plank, namely the technology of growing the species and efficient crop management, has been traced in Chap. 3. Ideally, these two planks are not just interactive but strongly synergistic, and both should be aimed at likely future markets. Some major changes in practices for growing radiata came after the late 1960s, and these were largely centred in New Zealand. In some respects the early genetic improvement and new growing practices meshed well, but in other respects they did not (Sects. 5.4.4.6 and 6.3.2.2), creating a fresh challenge to better integrate the two domains.

As with the ongoing genetic improvement, learning how to grow radiata as a plantation crop progressively better has been important, both in itself and as a path-breaking exercise in the development of late 20th-century plantation forestry with other species as well. The process was not always smooth and orderly, because traditional approaches often proved wanting, as did certain of the much-vaunted remedies (Sects. 5.4.4.6 and 6.3.2.2).

After large-scale harvesting began, restocking clear-felled areas was often a vexing task. It progressed from management of natural regeneration, through some use of direct seeding, and then usually to a commitment to immediate post-harvest planting. It was only after trial-and-error with restocking practices that planting became accepted or even mandated practice. In support of this, the growing of field-ready planting-stock was much improved by better and more intensive nursery practices, and the tending regimes for plantations were greatly intensified (Box 5.1).

Box 5.1 Regeneration Systems

Natural regeneration by seed can work spectacularly for radiata. However, both it and broadcast seeding give poor control over stocking and limited control over genetic quality. Therefore, planting of nursery stock has become almost universally preferred for establishing plantations of radiata. To this end, the raising and planting of nursery stock have been greatly refined.

5.4.2 *Crop Establishment*

5.4.2.1 Seed Collection

Radiata is one of the easiest of all commercial tree species for seed collection, even though its cone-bearing trees are often tall. The cones generally each contain over a hundred seeds, and can remain unopened on the tree for years (Fig. 5.1). In cool, moist climates, the trees can accumulate seed crops year after year, unlike many tree species in which good seed crops occur only occasionally and then need to be collected during narrow time windows between when the seeds are ripe enough and when they fall and scatter. Thus, while some of the seeds may be released by some cones opening in summer heat, radiata's closed cones typically provide a "seed bank" ready for release by fire or after climatic damage creates gaps in stands. While the cones remain closed, the seeds therein remain viable almost indefinitely, and even after extraction they store remarkably well (Shrestha et al. 1985).

This ease of seed collection is also of some help to breeders undertaking controlled pollinations. However, there is typically more than a two-year delay in

Fig. 5.1 Accumulation of ripe, unopened cones on a radiata graft within a hedged seed orchard

most pine species from pollination to availability of fully-ripened seeds, a drawback compared to the less-than-a-year delay in such species as redwood and Douglas-fir. Indeed, keeping that delay to only two years for radiata can depend on "curing" still-green cones picked early in order to accelerate ripening but retain full viability of its seeds (Rimbawanto et al. 1988).

5.4.2.2 Natural Regeneration

The accumulated seed crops on felled trees often allow natural restocking of clear-felled radiata plantations. After felling, the cones scattered in the slash can open readily to shed their seeds, especially with summer felling. Many of those seeds germinate successfully, especially if logging activities mix the seeds into the soil. This initially inexpensive option, however, has proved a mixed blessing. The genetic merit of the resulting crop was limited by that of the parent stand, although there were some benefits from earlier natural selection and if selection imposed by thinning of the crop was eugenic. Moreover, stocking and spacing proved hard to control. Stocking was often excessive and/or uneven (Fig. 5.2). Overstocking may require expensive thinning, and gaps may require infill planting. Lack of such follow-up management resulted in uneven diameter growth and variable knot sizes, which often led to reduced crop values.

At the other extreme, natural regeneration was sometimes inadequate, leaving areas of unstocked ground and/or trees that developed poor form. Reasons for inadequate regeneration were various, including excessive weed growth, felling the parent crop during winter (meaning that seeds do not get mixed with soil when cones open), burning the logging debris, and/or too much seed predation by birds and/or mice.

Fig. 5.2 Aerial view of part of Kaingaroa Forest, New Zealand, showing patchiness of natural regeneration of radiata occurring after clearfelling operations. Such natural regeneration is no longer relied upon, and is now discouraged

These problems with natural regeneration of plantations, in which regeneration often was over-dense, too sparse or unacceptably patchy, have occurred in all the countries that are the main growers of radiata as their plantation managers attempted to rely on natural regeneration.

5.4.2.3 Direct Seeding

Failing an assurance of good natural regeneration, managers sometimes spread supplemental seeds on the ground (called "broadcast sowing") in order to achieve restocking. This was sometimes done from aircraft following plantation harvest. Such broadcast sowing still left some problems of variable stocking. It also required the acquisition and use of large numbers of seeds per successful seedling, which militated against selection for better genetic quality.

It has proved possible to use drill-sowing of radiata seeds on open grassland or in other light vegetation, which was done successfully around 1930 over a significant area to help create the Kaingaroa Forest in New Zealand. This technique has also been used, but on site-prepared ground, with maritime pine in the sandy Landes region of south-western France. With broadcast and drill-sowing of seeds, follow-up measures are needed to achieve even spacing of seedlings at an appropriate stocking. In the 1960s, following aerial sowing of winter-felled compartments in Kaingaroa Forest, problems of uneven stocking persisted despite such follow-up. Because of these problems, and the desirability of making efficient use of more-expensive seed from select parents, aerial sowing was discontinued in New Zealand after 1971 (Levack 1973).

5.4.2.4 Nursery Practices and Transplanting

For the most part, radiata seeds germinate readily. Their germination can be hastened and made more uniform by stratification, which involves keeping seeds chilled and moist before sowing. After germination, growth in the nursery is typically rapid such that, in many climates, field-ready seedlings can be easily produced within a single year (Fig. 5.3).

By 1983 it was clear that radiata could be propagated on a large scale by rooting cuttings from very young seedlings and/or from low-hedged seedlings or still-juvenile cuttings (Fig. 5.4). While not as easy as with such species as willows or poplars, it was proving much easier than effectively rooting cuttings from the great majority of conifers. The many prospective advantages of being able to operationally deploy excellent, well-characterized clones (Libby & Rauter 1984) were prompting development of rooting technology and knowledge in Australia, California and New Zealand for radiata. Operational implementation with radiata, however, did not prove to be straightforward (Sects. 5.5.6; 6.8.2).

Seedlings and cuttings of radiata are easy to transplant into the field, even if bare-rooted. Provided the site is well prepared, the planting is done well and the weather is favourable, close to 100% survival can often be achieved.

Even so, it is desirable to get the planting stock conditioned, to help assure good survival even in adverse conditions, and good growth from the outset. An important advance achieved from research in New Zealand during this period was repeated undercutting of the roots in the nursery beds, to encourage fibrous multiple-root development and to harden off the tops so the propagules can resist some desiccation shortly after field planting. Such treatment is inclusively termed "wrenching," and begins by undercutting the tap roots of seedlings or sinker roots of cuttings.

Fig. 5.3 Nursery beds of radiata seedlings, showing green apical tufts of primary (juvenile) needles. With time and increasing height the shoot tips transition into brown, sealed buds

Fig. 5.4 Stem cuttings of radiata in nursery bed 10 months after collection from stool beds

It became appreciated that good initial field survival of planted propagules is not enough. Instead, rapid and uniform growth was sought right from the first year in the field, which required even-sized, robust and well-conditioned nursery stock. This was vigorously addressed by the New Zealand Forest Research Institute, especially during the late 1960s and 1970s (Chavasse 1969a, 1969b, 1973, 1976, 1981), these developments being encapsulated by Maclaren (1988) (see also Mead 2013). Better precision-sowing of individual seeds was developed as a basic step in obtaining seedlings of the right size and robustness. To condition the planting stock, and control planting-stock size, the traditional treatment of wrenching was much refined by repeated mechanical undercutting of roots and trimming of long lateral roots.

Good planting is of course also needed, not just to ensure survival and immediate growth. Getting the root system well configured and distributing the roots well in the soil can be crucial to avoiding young seedlings "toppling," particularly on windy sites with heavy soils. Such toppling results in swept and leaning stems that drastically reduce the value of the resulting logs (Fig. 5.5). Surprisingly, cuttings are much less susceptible to toppling, but cuttings-production technology was by 1983 not yet sufficiently advanced to exploit that feature. Meanwhile, much effort was directed at refining the planting techniques for seedlings, still the favoured propagule type as of 1983.

Improved nursery and planting practices, particularly the developing cuttings technology, were worthwhile in their own right, through reducing costs of subsequent tending, assuring better yields and log quality, and even making for slightly earlier harvest. In addition, these developments effectively complemented genetic improvement, with such vegetative multiplication allowing much more efficient use of scarce seeds of top genetic quality.

Fig. 5.5 Result of post-planting tree toppling, showing persistent butt deformation that greatly reduces tree value. Toppling can result from any or all of poor practice in the nursery, poor planting, soft and sticky soils and failure to consolidate cultivated soil

5.4.2.5 Site Preparation and Weed Control

For reasons indicated above, planting had by the late 1960s become very much the preferred option for both afforestation and replanting with radiata. Preparing ground for either operation serves one or more of three main purposes: controlling and/or killing unwanted "weed" vegetation (Fig. 5.6), including much that survived logging or previous land uses; ameliorating the soil; and mitigating harsh microclimates (Fig. 5.7). Clearing vegetation can take various forms, such as burning or crushing the logging slash, felling or crushing scrub and unwanted small trees, burning bracken fern, and/or use of herbicides to control various types of weed vegetation (Fig. 5.8). The soil can be ameliorated by such measures as ploughing or ripping to control vegetation and/or break up hardpans, and by additions of fertilizers. The near-ground microclimate can be improved for newly planted trees, for instance by creating raised soil beds, and/or by reduction or elimination of vegetation to allow better cold-air drainage and reduce the extent of surfaces that create radiation frosts.

Radiata's early rapid growth and its tolerances of some drought and of relatively low soil fertility mean that super-intensive control of competing vegetation is not

Fig. 5.6 Site preparation for planting achieved by mechanical clearing of existing vegetation, but involving some undesirable scalping of topsoil

Fig 5.7 Site preparation using a controlled burnoff of logging debris. While producing a clean site, often reducing frost hazard by improving cold-air drainage, this practice has been widely abandoned. On some soils it causes site deterioration, and it is always objectionable to the public. An alternative for controlling weed growth is use of desiccant sprays

Fig. 5.8 Spot spraying of grass before planting radiata, to avert competition from pasture grasses

required in its establishment phase. Even so, control of competing vegetation is sometimes needed after planting, to give the young trees enough light or to reduce competition for water and nutrients. Being tolerant of various herbicides, radiata in some countries featured in the development of mechanised (often aerial) post-planting applications of herbicides.

Intensive site preparation and follow-up weed control did not begin in the plantations of radiata. For growing certain tropical tree species (including hoop pine in Australia), where weed growth was typically luxuriant and aggressive, such practices were already traditional and intensive. The adoption of such practices for radiata, however, is of note for several reasons including the following three as examples: while not essential for achieving survival, the economic advantages of a rapid take-off were recognized as important; mechanisation of some of these operations was developed to a new level; and use of better selective herbicides (that killed most vegetation but did not harm radiata) came to the fore.

For re-establishing plantations after harvest, site preparation involved some different issues which centre around the use of fire. Burning of logging slash to clear sites for planting had several attractions, including low cost per hectare. In addition it can achieve one or several of: precluding unwanted natural regeneration, facilitating replanting, preventing outbreaks of insect pests that damage or kill young trees, and ameliorating the microclimate by allowing better cold-air drainage. However, in South Australia, slash burning was used largely to preclude over-dense regeneration. On those nutrient-poor soils, burning volatilized some nutrients and released others in a single pulse, allowing most to escape the site. The consequent loss of humus and already-scarce nutrients led to serious site degradation during the 1950s and 1960s. This degradation was halted and strongly reversed by abandoning slash burning, instead mechanically shattering and partially burying the slash, thus allowing a much slower release of nutrients that were mostly captured by the growing roots of the new trees. The sites were then improved by supplementing the on-site nutrients with applied fertilisers (Nambiar and O'Hehir 2010; O'Hehir and Nambiar 2010). On New Zealand's generally more nutrient-rich sites, slash burning had been widely adopted during the 1970s without the same ill-effects, but was later discontinued on environmental grounds, with public objections to the smoke and concerns over the eventual impacts on soils. In Chile, a common practice developed following slash burning that allowed farmers to grow wheat crops for a few years on the ash beds among the recently-planted trees; this shared the costs of site preparation and averted competition from certain weeds, but was to the further detriment of soils that had already been degraded before afforestation. Locally there, burning of logging debris has been observed by RDB to cause severe soil deterioration.

5.4.2.6 Spacing

Traditionally, based largely on earlier European practice, plantation forestry had usually prescribed planting trees at a much greater density than needed for the final crop that was to be harvested in a clearfelling. With radiata there have been at least two main reasons for this traditional practice: (1) for producing high-quality sawn timber, the dense early stocking gave control of branch size—and thence knot sizes in timber—especially in the lower logs that provide most of the financial value in a tree to be harvested for sawn timber; and (2) more importantly on some site types than others, dense initial stocking gave the forester a safety margin to allow for thinning out high percentages of trees with malformed boles or poor vigour, leaving the better-quality and more vigorous trees to grow on to harvest. In addition, suppression of weed growth was often a bonus from dense planting. However, adoption of very dense planting to allow for post-planting mortality is unsatisfactory; it does not address any underlying establishment problem, and usually leads to patches of both overstocking and understocking. Also, while not directly related to very dense initial stocking, the harvesting of thinnings was seen as a means of securing the advantages of early financial returns but, as we shall see later, the financial benefits depend on favourable cost and price structures at the time of thinning.

5.4.3 *Use of Fertilisers*

By the 1950s, substantial areas of radiata plantation in both New Zealand and Australia were growing poorly, even after correction of the dramatic problems caused by deficiencies of zinc (Sect. 5.2) (Fig. 5.9). In New Zealand, from about Lat. 37½°S northwards, many stands were extremely unthrifty. Phosphorus deficiency was diagnosed, and could be effectively corrected by aerial topdressing with superphosphate (Weston 1956, 1962; Conway 1962; Ballard 1977), that becoming routine practice on such sites by the early 1960s (Fig. 5.10). Application of phosphatic and other fertiliser, including nitrogenous ones, also expanded in Australia, notably on

Fig. 5.9 Five nursery seedlings showing zinc deficiency compared with one with deficiency corrected by spraying with zinc sulphate

Fig. 5.10 Response of radiata to phosphatic fertliser on strongly P-deficient site. The tree on the left is severely deficient; on right this deficiency has been corrected

phosphate-poor sites in New South Wales, the ACT and parts of South Australia (e.g. Boardman 1988; Horne 1988). That input, together with weed control, was sometimes sufficient to make radiata an economic crop on sites otherwise regarded as unsuitable for the species (Boardman 1988). Understanding of the interactions of fertilizer application with weed management, with thinning and with stand age led to appreciable gains in volume production (Australian Forestry Council 1981). The increased use of former "improved" pastureland for plantations was found to give rise to a new set of problems—soil nitrogen levels perhaps two orders of magnitude greater than those of unimproved pasture resulted in imbalances with several other nutrient elements (Horne 1988), plus ill-effects on tree form and wood properties.

In both South Africa and Chile, where nutrient deficiencies were often manifest in radiata, use of fertiliser applications came much later. South Africa continued to rely on maritime pine on its less-fertile sites within the Mediterranean climate zone, while in Chile the deficiencies tended to remain uncorrected in radiata plantations until after 1983.

5.4.4 Thinning and Pruning Regimes

Thinning commercial forest stands was long-established practice, aimed at removing cull stems and concentrating growth on the better trees to produce logs that are more valuable on account of both their quality and size. Pruning, in the form of removing lower branches, can be complementary to thinning. Low pruning, up to a height of around 2 m, has often been practiced to improve access and/or reduce fire hazard, with production of some clear, knot-free timber a bonus. Far less common had been pruning up to a full log length of 5–6 m to obtain much bigger yields of clear timber. Since cost-effectively producing such clearwood depends greatly on diameter growth after pruning, thinning and pruning practices need to be closely integrated.

The evolution of thinning regimes and the frequent adoption of pruning are important parts of our domestication story. With radiata, the application of the traditional approach of repeated thinnings, and harvesting the thinnings, had not been straightforward. Indeed, there are some intriguing paradoxes. Left untouched, dense radiata stands can progressively thin themselves from thousands of small young trees per hectare to about 200 or fewer large survivors as the stands mature. Luckily, those survivors tend to be better-formed trees, with low rates of forking and other malformation. Their near neighbours therefore become suppressed (overtopped) and, depending on the environment, those increasingly weakened trees readily suffer mortality due to natural causes. The trees that achieve local dominance thus create enough space for themselves to eventually make the diameter growth that is needed to produce reasonably valuable logs. That is what happened in the huge plantings created in New Zealand during 1925–1935, to a lesser extent in the Chilean plantings done mainly during the 1940s, and locally in Australia. Such strong assertion of dominance in radiata by a minority of trees is unusual among tree species. Nevertheless, radiata is still highly responsive to silvicultural intervention in the form of thinnings and pruning, but margins for error in the timing and execution are often small.

In New Zealand during 1938–1945, because of the Second World War, there had been neither the manpower nor the money available to do widespread thinning. A high proportion of the suppressed trees usually were destined to die in New Zealand, even without the additional mortality due to a late-1940s outbreak of a woodwasp that killed huge numbers of weakened radiata pines. In Chile, with its generally less natural stem mortality, a high proportion of suppressed stems could typically be harvested in the course of early clearfellings—where markets could be found for very small logs.

5.4.4.1 Some Problems with Commercial Thinning

By the mid-1960s, it was already known that, despite radiata's potential for self-thinning, its health and growth vigour are highly responsive to thinning and other interventions. An immediate problem, though, was that the financial returns from the typically small trees harvested in thinnings usually did not cover the costs of planning, felling, logging and transporting the numerous small logs produced. In New Zealand, A.R. Entrican, who during the 1920s and early 1930s had organised research on the utilisation of wood from radiata plantations (and later became head of the Forest Service), envisioned the thinnings strictly as pulpwood. But even when pulpmills opened and created markets for pulpwood, it was soon clear that the price and cost structures associated with most thinnings made their harvesting unprofitable. This was seen as partly because, even after the timber from the self-thinned early radiata plantations came on stream, the government (through the State Forest Service) continued to sell high-quality standing timber from native forests at artificially low prices, in the name of providing easily affordable houses (Orr 2017). That practice effectively ignored a key goal of the 1920s plantations, which was to have their wood substitute for native woods, in order to allow more native forests to be retained unharvested. In addition, mechanised harvesting of thinnings was still primitive, and not yet cost-efficient. Actually, some forest managers did just accept that young thinnings would not be profitable, and left the small felled trees to rot on the ground, often seeing that as a penalty of having planted too many trees in the first place. This issue prompted radical solutions (Kininmonth 1997a), which we will trace below (see Sect. 5.4.4.3).

In Australia, where wood supplies were often scarce and the terrain often easier, harvesting of radiata thinnings tended to be less of a technical and commercial challenge. On easy terrain, with the lower rates of stem malformation associated with Australia's lower average site fertility, a much cheaper and simpler approach to thinning would often work. In it, thinning out whole rows of trees could be done with little adverse effect on the quality of the final crop. The removal, for example, of all trees in every seventh row ("outrows") provided convenient access throughout the stands for modified highway trucks ("crane trucks"). Also, the timber markets often allowed small harvested logs to often be profitably sawn, for example for making boxes for fruit, as well as being used for pulp in some locations.

In Chile, where labour costs were much lower and bullock teams were available, with little tree mortality from suppression, it was common to make a profit on harvesting the considerable volumes of small, closely-spaced trees that comprised thinnings. Alternatively, unthinned plantation stands were often clearfelled quite young, meaning very little loss of wood to natural stem mortality.

It was in New Zealand, where competition-induced tree mortality was often high, that the conundrum of what to do about thinning was a pressing issue, and where a radical approach was developed. There are several threads to the story, in which a few foresters and scientists played key roles.

5.4.4.2 Some Lessons from South Africa

Long before the issue of thinning regimes for radiata was recognised as being so problematic in New Zealand, some ground-breaking research had been done in South Africa by I.J. Craib. A research forester with a doctorate from Yale University, Craib worked for the South African Department of Forestry. In the 1920s and 1930s, he was working with several fast-growing tree species including radiata, in a climate characterised by long dry periods. Among his studies was a series of spacing and thinning trials with the radiata. The results led him to prescribe planting at much wider initial spacings and heavier thinnings than previously used. Where they were adopted in South Africa, his prescriptions were a great success. Significantly, he cautioned strongly against letting thinning operations fall behind prescribed schedules, because that would lead to delays in logs reaching millable size, which would badly affected the projected financial profitability of South African plantations.

5.4.4.3 Towards Radical Changes in New Zealand Practice

In New Zealand, from the late 1940s, forester John Ure was overseeing the restocking and subsequent tending of large areas following clearfelling, after the harvesting of the 1920s plantations accelerated sharply in Kaingaroa Forest. He was mindful of experience with overcrowded stands planted before 1940, which were suffering heavy mortality from attack by the wood wasp *Sirex noctilio*. At the same time, he was often faced with over-dense natural regeneration, especially where stands had been clearfelled during summer. In response, he prescribed very early thinning of the natural post-harvest regeneration, to be followed by relatively few and heavy thinnings later on (Ure 1949) (Fig. 5.11), in the expectation that the later thinning could be harvested profitably.

Despite Ure's hopes, attempts at commercial thinning remained stubbornly unprofitable in most parts of New Zealand. The scene was set for a more radical approach (Kininmonth 1997a). In that, three key players were, in approximate historical order, C.H. Brown, E.H. Bunn and R.T. Fenton[1].

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[1] The remainder of this section is heavily based on personal recollections of one of us (RDB) who was in contact with Fenton and Bunn during the time period.

Fig. 5.11 Early trial tending natural regeneration in Kaingaroa Forest, New Zealand, showing heavy early thinning and low pruning

Brown was a forester responsible for areas in the far south of New Zealand where young plantations were at ages when decisions had to be made about their tending. He was well-acquainted with problems of trying to thin relatively old, over-crowded stands of radiata. Later on, he also noted the disastrously poor grades of sawn timber from a Corsican pine stand that had been thinned heavily to allow the crop trees free growth, but the resulting large lower logs had received only very belated pruning. In 1956 he therefore decided to focus thinning efforts on his young stands, and he realised he needed to address the questions of when and how to prune. In taking the initiative, he was even prepared to physically do experimental tending himself. In tackling the younger stands, thinning heavily and doing first pruning before age 10, his aim was to keep the "knotty core" of logs small so the butt logs would contain a thick outer zone of clearwood.

Bunn, to whom Fenton reported while researching thinning regimes, had had some important prior experience. In 1951, while waiting to attend the Forestry School in Canberra, Bunn was working at the Waipa State Sawmill in Rotorua and was given the task of tracking logs in the mill to identify categories that should be pulped rather than sawn. The result was a big surprise, in that he found that the large, rough logs from stand-margin trees tended to produce better grades of sawn timber than did the smaller, finer-branched logs from trees in the stand interiors. Another experience may have helped shape his outlook. At a New Zealand Institute of Foresters Annual Conference in 1960, which Bunn attended, J.H. Beekhuis was presenting research results from sample plots of radiata thinned to several regimes spanning what had been the range of accepted practice when he started out. Beekhuis was rewarded with a short but withering verbal blast from A.P. Thomson, who later became Director-General of the Forest Service. Thomson pointed out that the New Zealand Forest Service had already adopted heavier thinning regimes than any studied by Beekhuis. When Bunn later oversaw FRI's subsequent silvicultural research, he was guided by two strong, related principles: "be prepared for the unexpected," and "try a range of treatments extending beyond the bounds of any anticipated practice."

Those principles led Bunn to strongly support Fenton, and to exhort Fenton's juniors on those principles—at great length and sometimes late into the night. Fenton had been recruited in early 1962 by the Forest Research Institute, Rotorua, to study the Economics of Silviculture. He had previously worked in a sawmill in the same region as where Brown was working. He was acquainted with Brown's investigations, and shared with Brown experience of the results of very delayed pruning together with heavy thinning of Corsican pine.

Crucially, Fenton was not one to flinch from following an argument to its logical conclusion. He headed a team that worked on a broad research front. They relied largely on sawmill studies of sawn-timber grades from radiata stands that had received known treatments. New thinning and pruning studies were begun, log outturns from alternative tending regimes were projected from existing yield tables, and costs and returns for the alternative regimes were used for financial analyses.

Unavoidably, some important assumptions had to be made. A supply of good-length clear (knot-free) sawn timber of radiata was essentially non-existent at the time, while abundant clear sawn timber was still available from native forests in New Zealand. Thus there was no real market information on the value of clear radiata timber. On the other hand, large premiums for clear versus knotty timber of other pines were commonplace overseas, so it was logical for Fenton to assume that a similar premium would eventually prevail for clear timber of radiata. Since there was no real impetus from the wood-processing and building industries, the whole exercise stood as an example of technology-push rather than demand-pull.

On the silvicultural front, one notable trial, in northern Kaingaroa Forest, included a treatment thinning in one step to final-crop stocking of 200 stems per hectare, combined with immediate pruning of the trees left. The outcome was remarkable in that the resulting stand developed with good tree form, without unduly heavy branching.

Preceding their work on alternative radiata growing regimes was a detailed simulation study comparing the economics of developing an area of land into forest plantation versus pasture. That study had been based on accepted silvicultural and pastoral-development practices at the time, along with the then-current cost and price structures. But, once it was completed, Fenton and his assistants turned to re-examining the economics of alternative silvicultural regimes in search of ones that would be more financially profitable than the existing ones. This took the economic study of industrial forestry to a new level.

Certain of their modelled findings were clear-cut, and some of them were very surprising, especially to foresters of classical silvicultural training. Having adopted reasonable assumptions, their models indicated that afforestation with radiata could be financially competitive with the alternative of developing all the available land for pastoral farming, often projecting an internal rate of return from afforestation with radiata of over 7%. Their modelling also predicted that pruning of butt-logs to produce clear sawn timber could be highly rewarding if combined with sufficiently early and heavy thinning. In this connection, the second log, from 5–10 m up the tree from stump level, posed a problem, being too high to prune cost-effectively, even with economies of scale over large areas. Yet, those "second logs" were modelled as too large to treat as just a low-value by-product of producing high-quality butt logs. This meant that while improving the size and quality was largely in the hands of culturists, offsetting adverse effects of the lower stockings on branch size and general stem quality in the second and higher logs would be up to the breeders.

Perhaps most interesting, Fenton and his team found that delaying thinning until the trees were big and old enough to make the thinning immediately profitable could severely compromise the overall profitability of the crop. Such a delay in thinning reduced the average diameter growth in the remaining crop, in turn delaying the final harvest. Commercial thinning of older larger trees could also lead to substantial damage to the final-crop trees, further reducing the volume of wood that could be harvested at low cost per unit of generally more-valuable wood. In other words, waiting until a thinning could immediately return more than the thinning operation cost carried a major, if far from intuitively obvious, opportunity cost.

Accordingly, Fenton (1972) proposed the "Direct Sawlog" ("Direct") regime. It entailed more than one non-commercial thinning, leaving the thinnings to rot on the ground, and accepting significant sacrifice in total wood yield per hectare. The financial and productivity costs were justified on the expectation that the regime achieved greater full-rotation profitability with a major contribution from better-quality sawn timbers and veneers. Such a regime was indeed radical, but it underscored with much stronger data Craib's key tenet, namely that thinnings should not be delayed in hope of an immediate net profit on thinning.

The Fenton team's recommendations focused on getting the course of stand development firmly set during its first 10 years from planting, which is before post-thinning wind damage becomes a significant risk. All operations, including site preparation, spacing of initial planting, beneficial fertilization, thinning, pruning, and protection from competition and damage, were focused on the production of valuable sawlogs. They recommended using pre-commercial thinning pre-emptively rather than as a source of pulpwood, rejecting any notion that zero-revenue thinning should be a last resort in the absence of any profitable market for thinnings. That made pulpwood, mostly from upper logs, almost entirely a by-product of growing for solid-wood products. Despite much initial scepticism, the science-based data looked compelling, and the Direct regime became widely adopted. Often, however, the practices of Fenton's enthusiastic followers in New Zealand became even more extreme than prescribed in the Direct regime.

Actually, the results of Fenton's studies did not entail an unconditional proscription of commercial thinnings. Rather, those studies set a framework for identifying the various conditions that would have to be met for the option of commercial thinning to be truly economic, in the sense of contributing positively to the profitability of the crop over the whole rotation (Box 5.2).

Box 5.2 Thinning Issues

Thinning has traditionally been practised in forest plantations, providing some early wood yields, often harvesting trees that might die and rot before the final harvest, and concentrating wood production on the best stems that form the final crop. However, delaying thinnings until the extraction can be done at a profit can affect the economics of the final crop unacceptably, making it appropriate to thin early without harvesting the thinnings. Moreover, returns from pruning depend heavily on the "crop" trees having enough space in which to put on clear, knot-free timber after pruning. In New Zealand a combination of heavy, non-commercial thinnings and intensive pruning was widely adopted. Often, however, it was to compromise unduly—and more than anticipated—both the yields and wood quality of radiata.

At least three other factors helped adoption of Fenton's more radical approach. Firstly, with genetic improvement, many fewer trees needed to be planted per hectare in order to guarantee a final crop that would be composed almost entirely of trees of good form (Figs 5.12 and 5.13). Secondly, it was accepted that the benefits of pruning would be enhanced by stems being straighter, which was another consequence of genetic improvement. Thirdly, there came a realization that the early stockings needed to allow for stem malformation (even in genetically improved stock), in order to assure a well-formed final crop, would be less than had been feared. This was because mild stem malformation, in the form of forks or **ramicorn**$^{\mathbf{G}}$ branches was found to be very often self-correcting, although it would still cause some degrade inside the log. Some of the early stands thinned to Ure's prescriptions were found a few years later to have disturbing percentages of malformed tops which, because the self-correction rate among malformations was not yet appreciated, caused alarm at the time over aggressive thinning regimes. Importantly, the promulgation and later acceptance of the Direct Sawlog regime came when a second radiata planting boom was gathering momentum in New Zealand.

An offshoot of the move towards radical silviculture in New Zealand was an agroforestry movement in New Zealand (Maclaren 1988). This movement, while arising in parallel with a worldwide agroforestry movement, was mostly prompted by local factors. These factors included the disenchantment with commercial thinning, and much disenchantment with poor profitability of pastoral farming on large areas of hill country. A solution proposed was to convert from pure pasture to agroforestry by planting trees into problem pastures at low initial stockings. That would let sheep graze the pasture during the several years between when the young trees were large enough to avoid serious damage from stock until when the pasture grasses were suppressed by canopy closure. That way, "pasturage" would

Fig. 5.12 Tree stocking trial with the Direct Sawlog regime, all thinning done without waiting until thinnings were worth harvesting

provide an early financial yield in place of commercial thinnings. Where radiata was the tree species of choice, it was important that the young radiata pines proved to not be seriously vulnerable to damage by grazing stock. Furthermore, ex-pasture sites often gave very rapid tree growth because of the enhanced soil fertility that resulted from relatively intensive pastoral farming.

Neil Barr was a visionary and charismatic early farm forester of great enthusiasm, energy and affability, and he helped found the New Zealand Farm Forestry Association. Barr was a vigorous proponent of pasturage as a yield in place of thinnings, and was much emboldened after a team of workers pruned a young stand far more severely than he had intended, but with excellent results. Barr's farm, however, was in a locality north of Auckland where problems with tree form in radiata tended to be minimal. Many early recruits to agroforestry visited that farm, which perhaps led to some over-optimism.

Fig. 5.13 Stand grown under Direct Sawlog regime ready for harvest; early thinning to low final-crop stocking was accompanied by pruning

Fig. 5.14 Early stage of agroforestry trial with radiata, established in pasture with the idea that pasture could provide an intermediate yield in lieu of thinnings, prior to canopy closure

Major impetus for agroforestry research in New Zealand undoubtedly stemmed from a personal friendship between Bunn and Barr. Within FRI and with Bunn's blessing and support, Leith Knowles led early research efforts on the agroforestry option (Fig. 5.14), joined by personnel from the Ministry/Department of Agriculture. In the following three decades, Knowles made the results of that research broadly available, and joined Barr in strongly advocating the apparent advantages of agroforestry. The availability of genetically improved radiata with better stem form, while not specifically directed to uses in agroforestry, seemed to fit nicely the requirements of such widely-spaced farm forests.

Roughly paralleling refinements in establishing agroforestry blocks came refinements in the treatment of radiata shelterbelts to produce high-quality timber. Historically, shelterbelts had often been grown for producing firewood as well as providing shelter. This had often entailed periodic topping to control shelterbelt height, which also better maintained continuity of shelter and made the trees resistant to windthrow. Where the trees had not been topped they could produce respectable sawlogs. As radiata became increasingly accepted as a sawtimber, farmers became increasingly interested in producing quality butt logs material in shelterbelts. This led to a profusion of designs and management regimes for shelterbelts (Maclaren 1993; Mead 2013) (Fig. 5.15). For instance, some of the trees could be pruned for clearwood production, while intervening trees could be trimmed to produce continuing low shelter below pruning height; alternatively, the intervening trees were often of other, slower-growing species.

Fig. 5.15 Sophisticated shelterbelt grown on Canterbury Plains, New Zealand, by P. Smail, a prominent farm forester. The large trees are radiata, alternate trees being pruned for producing clear timber and left unpruned for providing continuous shelter. The smaller trees are deodar cedar, to give longer-term shelter from the ground upwards

5.4.4.4 Practice in Other Countries

Outside New Zealand, there was not the same rapid adoption of radical regimes, such as Fenton's Direct Sawlog regime, for a variety of reasons.

In Australia, there is typically easier terrain, which facilitated financially-viable commercial thinning; often less natural stem mortality from within-stand competition; an Australian focus on producing structural rather than appearance-grade timber; and often a declared management objective of maximising the volume of wood harvested per unit area (e.g. Jolly 1950). As it turned out, there often were problems with stands that had suffered as managers waited until a commercial thinning could be profitable. Silvicultural regimes did vary according to factors such as site characteristics, management policies, and availability and lucrativeness of outlets for young, small-diameter logs (e.g. Boardman 1988; Horne 1988; Lavery 1988). Even so, the different stand-management regimes adopted (Lewis and Ferguson 1993) have tended to be "incremental" modifications of classic, textbook practice. Thus much less pruning was practised, stockings tended to be kept higher and rotations were generally longer than in New Zealand. Exceptions included heavier thinning on low-rainfall, sandy sites in Western Australia (on which sites, however, maritime pine tended to be preferred over radiata), and in Tasmania where more aggressive tending regimes were sometimes adopted for radiata (Elliott et al. 2008).

In Chile, there had been some harvesting of thinnings in the early-1900s plantings, which were largely located near coal mines. However, in the large plantings that had been made later, especially those planted in the 1940s, very little silviculture was practised. Young trees in some areas had been pruned, but most stands had been left unthinned, as had happened in the stands established in New Zealand during the planting boom of 1925–1935. For utilisation of the wood, a modest-sized pulpmill had been commissioned in 1959, but this was later enlarged with three more pulpmills coming on stream during the early to mid-1970s as the large 1940s plantations matured. Compared with New Zealand, and even with Australia, between 1969 and 1983 Chile presented a very different context for silvicultural regimes to evolve in.

This Chilean context during 1969–1983 included a greater focus on efficient pulpwood recovery (associated with increasing pulping capacity), a high level of vertical integration between forest growing and wood processing; lower costs of harvesting of thinnings, less natural mortality in stands; and felling of stands at somewhat younger ages and thus producing smaller sizes than in New Zealand and Australia. While some stands had been pruned for clearwood production, silviculture has overall been more conservative than in New Zealand (Mead 2010, 2013). Compared with New Zealand, initial stockings in Chile were still typically higher, and pruning, when it was done, was less aggressive, as were thinnings. This was helped by natural, competition-induced tree mortality being comparatively low in Chile (Fenton 1979) (Fig. 5.16). Some Chilean radiata crops were even being grown exclusively for pulpwood, depending on the nature of the crops that then could be grown satisfactorily on the particular sites and the locations in relation to the pulpmills.

Fig. 5.16 Unthinned radiata stand in Chile, some 20 years old, showing relatively low natural stem mortality characteristic of Chile. Note the contrasting frequencies of branch clusters between the tree in the left centre foreground and one in the far right foreground (Photo W. Sutton)

5.4.4.5 Longer-Term Follow-up

Following on from Fenton's work in New Zealand, one of his team, W.R.J. Sutton, vigorously promoted the production of clearwood by the silvicultural regimes developed by the team. The assumptions driving the rationale at the time were two-fold: (1) such clearwood sawn timber would soon command much better prices than knotty structural timber; and (2) growers of radiata in several countries, especially those in New Zealand, would continue to enjoy a big comparative advantage for growing such clearwood timber because of radiata's outstanding growth rates and suitability as a plantation species.

Later, in 1979–1982, Sutton was charged by Bunn with leading a NZ Forest Service Task Force to model the growth and outturns of radiata stands under various site conditions and growing regimes. That team effort produced a software package, SILMOD, which was released in 1983. An important development supporting plantation forestry, SILMOD became a widely used decision-aid for forest planners and plantation managers. The SILMOD software has been updated and extended over the years, being superseded in NZ first by STANDPAK in 1997 (Kininmonth 1997b), and then by “forecaster” under the Scion software development company ATLAS. Such data-based decision-aids have been another leading-edge development in both plantation forestry and the beginnings of forest-tree domestication worldwide.

5.4.4.6 Tending Regimes in Perspective

Revisions of tending regimes were influenced not only by information on how different regimes had performed or, with increasing experience with them, how they would perform. They were also based on perceptions of what sites would be available for planting and what genetic improvement would achieve. Even with accumulating data on performance, making some important assumptions was still unavoidable. While some of those assumptions were explicit and consciously made, others were being made unwittingly. Some of the assumptions later proved to be wrong. This led to some disappointments with the performance of tending regimes adopted, and also with some of the selection criteria used in breeding. Moreover, these disappointments revealed some misalignments between silvicultural practice and the selective breeding. Details will be covered later, but the misalignments that later emerged are previewed briefly here.

By 1983 in New Zealand, accumulating experiences with the more aggressive Direct Sawlog and Agroforestry regimes were starting to reveal previously unrecognized limitations in what could be achieved by selective breeding, and to expose how genetic improvement of wood properties could be far more crucial than had been anticipated under such regimes (Sects. 5.4.4.6, 6.3.2.2, 6.7.2.4 and 6.10.1).

In Australia some misalignment between breeding and plantation siting had occurred, despite less aggressive silvicultural regimes. That was because early plus-tree selection there had mostly been done in heavily stocked stands on quite infertile sites. Yet the resulting seed orchards often went on to serve plantings on sites where fertility had been elevated by prior pastoral farming or by fertilising the plantations. That exposed serious problems with tree form (Birk 1990, 1991) when the offspring of those orchards were grown on such sites. As a result, progenies of NZ clones that had been selected on higher-rainfall and more-fertile sites were later found to be better suited to many NSW sites than offspring of NSW selections.

In Chile, the early preferences of harvesting for pulpwood had contributed to less aggressive silvicultural regimes than became fashionable in New Zealand. There the breeding programme did not pursue the option of breeding for longer lengths of knot-free timber without needing to prune (namely for “long-internode” trees), which seemed regrettable, because such trees appeared to be satisfactory for a wide range of Chilean sites (Burdon 1978). However, the eventual arrival of the European pine shoot moth (Sect. 6.3.1) would likely have nullified that advantage, because such trees are affected worse by leader damage.

5.5 Genetic Improvement

5.5.1 Operational Breeding Activities

We first outline major developments in operational breeding during the period 1969–1983 before later addressing their technical aspects in more depth. Some of the ongoing or routine activities, such as continuing seed-orchard establishment and replacement that did not entail important changes or advances, are not automatically reviewed.

Advancement through the first two generations of breeding had initially been relatively slow, partly through some false starts, such that selection and testing of genetically improved radiata pines had by 1983 seldom if at all proceeded past a second generation.

5.5.1.1 Australia

At the beginning of the period of interest in this chapter, a review of seed procurement for radiata plantations concluded that "seed collection is typically made from trees felled in routine thinning operations [of] older stands [in which] one or two thinnings would have already been carried out, thus removing the poorer fraction of the stand ..." During the period, seed production from first-generation seed orchards increased greatly, although production was variable between orchards and from year to year (Pederick and Brown, 1976). In some planting programmes, deficits in the supplies of orchard seed were offset by collections from clear-felled trees in heavily-thinned plantations and, in some cases, from specially-treated seed-production stands.

By the early 1970s the South Australian and Queensland forest services were then and subsequently able to use only improved planting stock from their own breeding programmes for all their radiata afforestation and reforestation (Wu et al. 2007). Cone collection, however, became difficult as the trees in established orchards increased in height. Pollarding (cutting back the upper crowns) was explored as a means of both increasing seed yield and keeping cones sufficiently accessible for collection, but neither goal was thus achieved (Matheson and Willcocks 1976; Pederick and Brown 1976). It became evident that the fiscally-useful life of radiata trees in seed orchards did not extend much beyond 20 years. The consequent decline in cost-effective seed-harvest had not been fully anticipated in at least some of Australia's radiata breeding programmes, with the result that some shortfalls in supply occurred during the 1970s and 1980s before new orchards came into production (e.g. Johnson et al. 2008). Nevertheless, by 1983 half of Australia's state forest service radiata planting programs were based on orchard seed only, and in others the fraction ranged between 70% and 82%.

As in New Zealand, it became clear that choice of site was a critical factor for a successful orchard. The radiata orchard at Mt Schank near Mt Gambier (SA) proved to be on an excellent site, and it provided notably high seed yields as well as good information on favourable orchard-site characteristics for radiata in Australia: temperate (maritime) rather than continental temperatures and a favourable soil moisture regime. At some locations with previously-established seed orchards, seed yields were substantially increased, and costs per seed reduced, by the application of fertiliser and/or irrigation. In some orchards, foraging by parrots (cockatoos) substantially reduced seed yields.

Using information from progeny tests, most of the radiata clonal seed orchards established during the 1950s–1970s had by 1983 been only lightly culled (less than 30% of the parent clones removed). The need to replace old orchards to facilitate seed collection also afforded the opportunity to use advanced-generation clones in them; by the early 1980s three of Australia's eight radiata breeding programmes were able to plant new orchards with second-generation clones, and most of the others were preparing to do so. This step was possible because early progeny tests attained sufficient age to permit assessment, and capacity to process the extensive data from them was greatly improved by better access to computers and evolving software for managing data and assessing breeding values, and for managing adverse genetic correlations (e.g. Cotterill and Jackson 1981; Dean et al. 1983). Their breeding objectives maintained an emphasis on improving growth, branching habit and bole form, although tolerance to drought was added in a secondary program in South Australia and resistance to diseases was sought in several programmes (Ivković et al. 2010); and APM recognised the importance of wood density in Gippsland, adding its improvement as a breeding objective. An Australia-wide genotype-by-environment interaction study established in 1969 and 1970 did not reveal interactions large enough of be operational importance among the genotypes and sites studied (Matheson and Raymond 1984).

Work in Australia (and New Zealand) was stimulated by field tours and discussions during and after the previously noted Third World Consultation on Forest Tree Breeding, held in Canberra in 1977. That meeting was sponsored jointly by the Food and Agriculture Organization of the United Nations (FAO) and the International Union of Forestry Research Organizations (IUFRO). A series of consultations and ongoing interactions through the working parties of IUFRO, both before and continuing after the 1977 Canberra meeting, has made important contributions to the development and conduct both of tree breeding and relevant international cooperation over the half-century from 1960 to 2010.

As in New Zealand, reviews of strategies for advanced selection led to the conclusion that most of the radiata breeding programmes had too few selections available as the founding parents for long-term breeding. Remedial steps included additional selections in then-established Australian plantations not previously evaluated and acquisition of seeds from other programmes, for adding to breeding populations.

The Woods and Forests Department of South Australia's radiata breeding programme was by 1969 being led by Bob Boardman and assisted by Forestry and Timber Bureau/CSIRO staff at Mt Gambier. At the commencement of the period considered in this chapter, that programme followed the basic Scandinavian model, but in the last third of the time a new round of selection in plantations added 627 first-generation plus trees (selected in unimproved land-race stands) to those already on hand to better provide diversity for later generations of breeding. Observations of the value to breeding programmes of good planning, and the greater availability of the information necessary for more complex work such as index selection (Cotterill and Dean 1990), led increasingly to the preparation of formal strategies and plans for genetic management that could be discussed, critically reviewed and periodically revised (Cotterill 1984)—a desirable practice that has been often emulated elsewhere.

Unfortunately, some of the serious forest fires in February 1983 (Sect. 5.1), in the Green Triangle and Adelaide Hills in South Australia, destroyed the major radiata seed orchard in the former area and other breeding resources, including progeny tests and clonal archives of plus trees. Thereby, it set back the breeding programme in the region by more than five years.

In Victoria the Forests Commission had hoped that by the end of the period there would be sufficient orchard seed from its breeding work, led by Leon Pederick, for the whole annual planting programme. Unfortunately, a 30-ha first-generation orchard at Campaspe—one-third of the commission's orchard estate—was burnt early in 1983. Accordingly, replacement seed was collected from old stands clearfelled because of fire damage, and was supplemented by large-scale multiplication of nursery cuttings of small quantities of seed-orchard seed. APM Forests in East Gippsland, primarily interested in pulp production, in collaboration with CSIRO wrestled with the negative correlation between volume production and wood density (Dean et al. 1983). Controlled pollinations were made between members of high-volume families and of high-density families, including selections from the Guadalupe provenance. Under the leadership of Mike Hall and John Cameron, they also maintained their seed-orchard programme, and a broad range of research related to vegetative propagation and stand management.

Seed for the very large New South Wales radiata planting programme was mostly derived from three seed orchards—Tallaganda (4.4 ha established 1957–1973), Green Hills near Tumut (17 ha, 1961–1969) and Vulcan, near Bathurst (67 ha, 1966–1972) (Johnson et al. 2008). Progeny tests of first-generation selections were assessed in 1977–1978, and the data used for culling the Green Hills and part of the Vulcan orchards soon afterwards. A new round of selection in land-race stands, during1980–1986, yielded 347 additional first-generation plus trees. Also, progeny trials seven years or more in age provided a further 240 select trees for the breeding population. Between 1979 and 1982, four large progeny and provenance trials, including the then-recent collections from natural populations, were planted within the state.

Queensland's commitment to breeding radiata continued, albeit at a low level because of the limited prospects of developing a large radiata estate in that subtropical, summer-rainfall environment. Trials including first-generation New Zealand progenies (planted from the late 1950s) and NSW Tallaganda (1970) progenies indicated that growth of progenies of trees selected locally was relatively inferior, probably a consequence of the nature of the local founding plantation population. Although no radiata seed orchards were reported by Queensland in a national survey in 1976 (Shepherd 1977), "local improved seed was available in the 1960s" and an orchard was planted in 1981 (Wu et al. 2007). Eventually, however, Queensland abandoned its own radiata breeding programme.

In Tasmania, the state forest service and a private company (APPM Ltd) established four orchards totaling 18 ha by 1976, in general following the Scandinavian first-generation protocols. Then, in the early 1980s, seedlings from more than 250 open-pollinated (mainly) and pair-cross families from programmes in Australia and New Zealand were planted in progeny trials. These were established to provide for selecting trees to produce a greatly expanded and more diverse base breeding population, to provide performance data for informing future breeding, and in the expectation that at least some of the included families would prove to be sufficiently adapted to Tasmanian conditions for near-future within-family selection, amplification and deployment (Elliott et al. 1995).

In Western Australia the Forests Department began planting a radiata seed orchard in 1965, using a minimal Scandinavian protocol because of uncertainty about the role of radiata there. Establishment of a second orchard, at Manjimup, was completed in 1972. While awaiting seed production to commence in this second orchard, seed was obtained from a heavily-thinned and fertilised 40-year-old stand by felling. As elsewhere, early selections in WA for seed orchards were on the basis of vigour and stem form. In 1978, however, the programme took the distinctive step of researching and breeding for improving resistance to the troublesome root pathogen *Phytophthora cinnamomi* (Butcher et al. 1984). Not only was within-population resistance (actually, tolerance) identified, but the previously neglected Cambria population was shown to include a high percentage of tolerant trees. Testing of Cambria trees was extended with a view to their inclusion in the breeding population (Wu et al. 2007).

A further round of seed collections of radiata, from ecologically-diverse natural stands across the entire natural range of the species, was undertaken in 1978, primarily to serve Australia and New Zealand (Sect. 5.5.4.1 below; Eldridge 1978).

5.5.1.2 New Zealand

A major expansion in the breeding population was begun in 1968 with selecting afresh an intended 600 plus trees in unimproved stands 12–18 years old (Shelbourne 1986; Burdon et al. 2008). For obtaining so many plus trees, the intensiveness of selection was reduced to the best tree in each 1.2 ha. Establishing and assessing three huge resulting open-pollinated (OP) progeny trials planted in 1969 was a major commitment for the FRI tree breeders. Those trials were established from cones collected from each of 588 new plus trees at the time the trees were found and selected in 1968 (Shelbourne et al. 1986; Burdon et al. 2008), resulting in around 30,000 OP offspring trees at each of three sites. Several purposes were served: testing the plus-tree parents, estimation of genetic parameters (variances, heritabilities, genetic correlations between traits, and the magnitude of genotype-site interactions), and providing a basis for forwards selection among the offspring. In the event, forwards selection was confined almost entirely to just one of the three sites, with the nearest and best-quality progeny trial. First assessment of the three trials was done in 1975, five years after planting out year-old seedlings, giving some research information, an early growth-and-form basis for an initial culling from those 600 parent clones in archives/orchards, and a very early selection of individual offspring for further testing. Of the 588 parent clones (a few were not grafted successfully), 250 were provisionally incorporated into fresh seed-orchard plantings on the basis of that very early assessment (Shelbourne 1986; Vincent 1986). Taking increment cores from progeny, those 250 parent clones were evaluated for corewood density, with about the lowest 50% culled on this basis (Shelbourne 1986).

As for the OP offspring, they had non-select male parents that were essentially random and virtually all different from each other. However, the very large number of half-pedigreed families with a total of many thousands of offspring provided a major advantage for belatedly including a new and high-heritability trait for selection, namely wood density. Previous work had already established that the high heritability of corewood density (≥0.5) was substantially greater than heritability for growth (ca. 0.2) (Burdon 1992). Accordingly, among offspring provisionally selected on both family- and individual-tree performance for growth and form, those with above-average corewood density were chosen. Those higher-density offspring trees were used for new seed-orchard plantings, and for intercrossing to produce the next generation of what was thus a new breeding population, to serve as a candidate population for a new generation of breeding (Shelbourne et al. 1986).

One hundred such “forwards” selections were made in 1975 and these seedling trees were then used immediately for controlled crossing *in situ* (that is, where each tree stood in the progeny trials). This was a laborious operation, but it saved time: in retrospect it proved to be in a very fortuitous time window when most trees were sexually mature but had not grown too tall. Two years later, seeds were extracted from these cones, germinated, and planted the following year in full-sib progeny trials. In the next few years, however, many of those 100 selections became badly affected by a needle-cast disease caused by *Cyclaneusma minus* (Fig. 5.17), despite good health at the time of selection. Accordingly, in 1980 nearly 200 additional trees were chosen in the same type of selection from one of those 1969 OP progeny trials, but with heavy emphasis on crown health and less emphasis on wood density. Those 200 selections were archived as grafts and later used for controlled crossing.

By 1980, largely in order to reduce evaluation costs, wood density was becoming assessed indirectly, more quickly but with lower accuracy, first by torsiometer but later by penetrometer tools applied directly to the candidate-tree boles.

A concern existed among breeders that the 1968 selections, which had explicitly favoured the short-internode branching habit, would preclude the option of obtaining good lengths of clear timber between knot clusters in unpruned logs. So in 1970 and 1973, a total of 140 plus trees was selected for a long-internode branching habit from within the same base population, and OP progeny trials were similarly established from them. In effect, a separate breed was thereby created.

Fig. 5.17 Cyclaneusma needle cast affecting several trees in the left foreground in a young radiata stand near Rotorua, New Zealand. This condition can severely affect growth rate, and resistance is now routinely sought in selection in New Zealand

Further controlled crosses were made around 1980, choosing parents on the basis of accumulated progeny-test information. Those crosses involved several series of select parents, and progeny trials were duly established.

In addition, several other sets of field selections were made for different special purposes (Sect. 5.5.2), but the programmes were later dropped because the effort and resources needed later proved on various counts to be unwarranted.

Assessments continued on other trials that had been established before 1969, yielding mainly research information on quantitative inheritance of a wide range of traits (e.g. Burdon 1992). That included encouraging evidence of worthwhile heritable variation in resistance to *Dothistroma* (Wilcox 1983).

5.5.1.3 Chile

The ill-fated breeding programme of Instituto Forestal (Sect. 5.3.4) involved selection in the early 1970s of some 200 plus trees from land-race stands over a wide area. This followed much the same protocols as followed in New Zealand in 1968, opting for fast-growing, straight-boled, small-branched trees with a short-internode branching habit. Clones were archived, and Instituto Forestal collaborated with one company that wanted to establish its own seed orchard. Unfortunately the practices that worked with initial archiving failed in trying to establish the orchard, so the grafts almost all perished. The OP seeds collected from those trees were stored for a while but, in the confusion of the time, were then all mixed together for sowing in a nursery.

Soon after the establishment of the breeding Convenio in 1976, eight member-company seed-orchard programmes were launched, with some others soon to follow.

In the Convenio, each member company was planned to establish its own clonal seed orchard, each orchard containing 40–44 plus-tree clones. Those clones were selected independently, where possible from each company's own local plantations, but on essentially the same criteria as the Instituto Forestal's previous selections (and the 1968 New Zealand selections). Importantly, much was learned from New Zealand's less fortunate experiences of orchard siting, with similar siting mistakes thus avoided in Chile.

A disadvantage, or at least difference from developments in New Zealand, of having separate independent company programmes, was that management of radiata's genetic material was not integrated across the country's radiata estate. This persisted despite counsel (Burdon 1978) that research be done on how well plus-tree progenies of each company performed on other companies' lands compared with on its own lands. But Zobel, who had originally been consulted, may have feared that most or all companies could be tempted to concentrate on a very few top-ranking parent clones at the cost of reducing genetic variation that would be needed for the future; anyway, he advised the Chileans to keep the companies' breeding programs and individual base-populations separate.

The Chilean focus on only the short-internode branching habit, while arguable, was defensible, since there was then no established market for clear sawn timbers in or from Chile. However, the long-internode trees in Chile often had far fewer tree-form problems than those on New Zealand's more fertile sites.

5.5.1.4 South Africa

Although South Africa's radiata breeding programme remained in place after 1969, based at Saasveld, the levels of financial and breeder commitments to it were limited. This reflected the fact that radiata was only one of five important pine species in South Africa's production-forestry sector, and it was grown over much smaller areas than in New Zealand, Chile or Australia. Moreover, interest was starting to increase in genetic improvement of eucalypts, with more financing and staff allocated to the eucalypt programmes. While South Africa followed New Zealand and Australia after 1968 in using many more clones in new seed-orchard plantings (van Wyk and Roeder 1978), no development of central importance to radiata's domestication occurred there between 1969 and 1983.

5.5.2 Structuring and Reshaping of Breeding Programmes

Radiata breeding programmes, in the countries where it was grown widely, tended to be divided into geographic units. With time, however, some geographic divisions were revised, while specialization according the breeding objectives began.

In Australia, the politically separate radiata breeding programmes of the various states imposed some degree of regionalization, however fortuitous or biologically imperfect that diversification might be in terms of rational and efficient domestication. On the other hand, the more lucrative markets for radiata logs in Australia remained quite narrowly based, being very predominantly used for light structural sawn timber. While several abundant eucalypt species (Eldridge et al. 1993) provided sawn timbers with strength and durability that excelled radiata timber, those timbers posed many more problems with sawing and drying than softwood timbers do. Those considerations contributed strongly to the national policy decision to greatly expand the softwood timber resource.

In South Africa, growing radiata was confined to more fertile sites in a restricted climatic zone in southern Cape Province. As in Australia, the more lucrative markets for radiata included light structural timbers for which it was the preferred pine species.

In Chile, the organization of radiata breeding within the Convenio involved company-programme independence, which led to a high degree of regionalization. Nevertheless, all those different radiata breeders employed similar foci on selection for traits important for light structural timbers despite the heavy emphasis on pulp production.

In New Zealand, the wide geographic scope of FRI's single radiata breeding programme had initially prompted internal regionalization of plus-tree selection and clonal composition of seed orchards. However, by 1983 this particular regionalisation appeared to be groundless for radiata. Data from plus-tree progeny tests replicated in very different parts of the country gave similar rankings for the same sets of progenies with respect to early growth and bole form. In other words, there was limited genotype-by-site interaction in those few traits and, as of 1983, separate breeding programmes and seed orchards were thus deemed "not needed" for either the North or South Islands.

On the other hand, New Zealand tree breeders had been uneasy about the exclusive focus on a "short-internode" branching habit, hence the decision to mount a smaller "side programme" based on selecting long-internode plus trees (Sect. 5.5.1.2). True, the high heritability of branching pattern, and favourable genetic correlations of more and shorter with growth rate and general tree form, had led to selecting for that branching pattern as a means of not only controlling branch size but also of improving other aspects of bole form (in a classic case of **indirect selection**^{G}). Yet given an established market for **clearcuttings**^{G} between defects in sawn timber, a continuing supply of long-internode logs produced without pruning was attractive. Long-internode genotypes would serve the option of being able to obtain useful knot-free lengths cut out from between clusters of knots in unpruned logs. Field observations of the long-internode trees that occurred in most plantations indicated that there were some sites, usually with lower fertility, where the long-internode trees would not incur serious bole-form problems.

Accordingly, in 1970 and again in1973, plus trees were selected specifically for a long-internode branching pattern, in addition to good growth, bole form and

Fig. 5.18 Radiata trees showing contrasting branching habits: "short-internode" (left) and "long-internode" (right). The former was pursued automatically in the mainstream breeding programme in New Zealand, despite giving only short lengths of clear timber between knot clusters, while the latter was pursued in a side programme to provide good lengths of clear timber without pruning, despite disadvantages in early growth and tree form (From Burdon 2004, permission Elsevier)

general health. Of the 140 such selections, 104 were selected in 1970 in northern Kaingaroa Forest, in the same general areas where the 1968 plus-tree selections favouring short-internode trees had been made. Fewer long-internode than short-internode plus trees could be found per unit area because of a combination of two factors: trees of the appropriate branching pattern were less common, and among them fewer had both high vigour and superior bole form. The remaining 37 such selections came from individual long-internode offspring within controlled crosses among plus trees selected in the 1950s. The long-internode selections and their offspring came to be recognized as a **Long Internode (LI) breed**, with a differentiated breeding goal that was primarily defined by the long-internode trait (Figs. 5.18 and 5.19). Clonal archives of these LI plus trees, and an LI seed-orchard and LI progeny tests were established. Strangely, no demand for seed from that orchard ever materialised.

The first-generation plus tress and their offspring in the mainstream (short-internode) FRI breeding programme then came to be designated the **Growth and Form (GF)** breed. A desire to acquire greater resistance to dothistroma (red-band) needle blight led to creation of a **Dothistroma Resistant (DR)** breed. That was

Fig. 5.19 Open pollinated offspring of long-internode radiata trees in a 15-year-old field progeny trial on a New Zealand site of moderate growth rate

first developed as an offshoot of the GF breed although, in the FRI programme, dothistroma resistance later became part of its mainstream breeding goal rather than the basis of a specialized breed. Some selections for dothistroma resistance, imported from Kenya, did prove to have superior resistance, but had not been selected for bole form and were therefore not integrated into the FRI breeding programme.

Two other specialized selection programmes were embarked upon experimentally in New Zealand, but both were abandoned, largely because the needs served later proved to be insufficient to justify the effort.

In New Zealand, some experimental selections were made in 1969 and 1970 for resistance to shoot dieback caused by *Diplodia pinea* (syn. *Sphaeropsis sapinea*). Despite indications of success (Burdon et al. 1982), there were no significant recurrence of the disease outbreak that prompted the selection for resistance (Burdon 2011), so the programme lapsed.

Provisional selections for frost resistance were made in 1973 in New Zealand, following a severe unseasonal frost. But, despite supporting evidence of genetic variation in New Zealand trials (Menzies et al. 1987), and strong evidence of heritability in California trials (Hood and Libby 1980), silvicultural research proved that the New Zealand frost problem could be overcome just by good nursery and establishment practices. In northern California, plantings of radiata on cold sites were abandoned due to the western gall rust epidemic raging in earlier radiata plantations there.

In Queensland, Australia, where hailstone damage to radiata provided entrance wounds for diplodia-associated dieback, the forest service had before 1950 selected for resistance to the disease, but this programme also lapsed, largely because of a combination of limited response to selection and the modest scale on which radiata was being grown in that state (Wu et al. 2007).

5.5.3 Tree-Breeding Strategy and Quantitative Methodology

The experience and theory concerning need for greater genetic diversity in the breeding lines that led to largely re-starting the New Zealand breeding programme in 1968 was a key prompt for forest tree breeding worldwide, with many species, to adopt a more strategic approach to forest tree breeding. Given the long time-frames involved, it was all too easy for tree breeders to find themselves “painted into a corner” through making strategic mistakes, having to essentially start afresh after many years, in order to assure good continued progress.

While early delivery of usefully-improved planting stock was needed in order to satisfy the accountants as well as foresters’ demands for improved planting stock, thoughtful tree breeders were by the late 1960s increasingly considering how to provide for continued genetic improvement in the long term, and how to prepare for enforced changes in breeding goals. Changes in goals could come from various causes, such as political or managerial fiats, different markets, new wood-processing technologies, better financial or genetic information, or crises resulting from new and serious pests or diseases. For the short term, using the best available information on heritabilities and other genetic parameters, breeders needed to predict magnitudes and net values of genetic gains under alternative mating designs, progeny testing systems and selection scenarios. The need for such projections was driven not only by breeder curiosity and for better fiscal efficiency, but to satisfy people in both industry and government that they would get value for money spent on tree breeding. As was documented by Shelbourne (1969), such projections followed on from the theoretical quantitative genetics work of Namkoong and his American colleagues (Namkoong et al. 1966). For the longer term, early choices of mating design and overall population structure were typically crucial to laying the foundations for future genetic changes in the service of effective domestication. Choice among mating designs was complicated by the fact that no one design can efficiently serve all the various purposes of these designs (Burdon and Shelbourne 1971; Zobel and Talbert 1984). This led to the suggestion that a combination of mating designs may be best despite additional costs (Burdon and Shelbourne 1971).

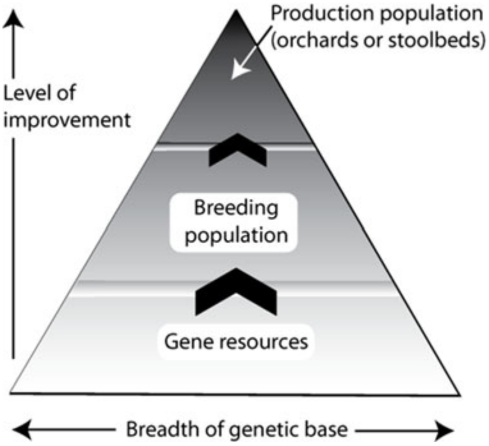
By the early 1960s, North Carolina State University (NC State) at Raleigh had become internationally recognised as a powerhouse for both quantitative genetics and experimental statistics. Zobel's industry-university-government tree breeding cooperative was then well-established on the Raleigh campus as a model operational programme with loblolly pine, and it served as a dominant training ground for both students and experienced tree breeders from around the world.

Several mating designs had been developed in service of the ongoing domestication of corn (maize) or chickens. The so-called **NC-1** was a hierarchical design for corn, which like pines is monoecious, bearing separate male and female organs on the same plant. NC-1 nests groups of three or four (preferably random and unselected) plants serving as "females," the plants in each group mated to a single different "male" from an independent set of plants. This produced groups of full-sibs with half-sib relationships through the males in common, useful for estimating additive genetic, some non-additive genetic, and environmental components of variation, which were in turn useful for estimating narrow-sense (additive) heritabilities and parts of broad-sense (total) heritabilities.

The so-called **diallel** design was also available, in which small groups of (usually 8–10 random) plants are all mated to each other serving as both males and females, including selfs. From this theoretically elegant design, narrow-sense heritabilities, inbreeding effects, maternal effects and (if the sibs are cloned) broad-sense heritabilites can be accurately estimated, although for groups containing few parent plants. It was a difficult design to complete, and few forest-tree programmes adopted it. (The Norway spruce programme at Aas, Norway, managed to complete and analyse three of them.) For a decade from 1976, under the auspices of CSIRO and STBA, 21 sets of 6 × 6 half-diallel crosses were made among radiata selections in Australia by RWG 1 members to provide second-generation selections for seed orchards and information to assist strategy development.)

The so-called **NC-2** design, an elongated factorial, employed very few (usually only four or five) tester "males," each mated to all candidate plants as "females." It achieved, through subsequent progeny testing, a fair and accurate evaluation of those candidate plants as parents for backwards selection. But it is terrible for forwards selection, because half of the next generations' genes come from those four or five sexy tester "males." Both the NC-1 and NC-2 designs were initially adopted by Zobel's programme for loblolly pine, and by many or most of the students trained in it. Both designs worked well in the first generation of domestication of various tree species, but both were inadequate for forwards selection in subsequent generations. In hindsight, it was adapted to the fact that a rooster could sire vast numbers of offspring compared with the finite numbers of eggs that individual hens could lay. It was certainly not designed to capitalise on the fact that a monoecious conifer could, especially after clonal propagation, produce huge numbers of seeds. While controlled crossing of seed parents with single pollen parents was possible, wind pollination meant that seeds of a particular parent could be sired by a virtually random collection of pollen parents from a large population—a phenomenon of great importance and convenience for the breeder.

Fig. 5.20 Schematic diagram illustrating the trade-off between level of genetic improvement and genetic diversity in a population "hierarchy."



Later, a **single-pair** mating design was developed that anticipates forwards selection through progeny trials. It mates half of the selected plus trees as "females," each with a different plus tree of the other selected half as a "male." It thereby optimises genetic diversity and value for selection among the offspring to produce the following generation and provide a genetically broad pedigreed base for later generations (Libby 1973).

During a year-long 1971 sabbatical visit by Libby to New Zealand, the concept of organizing genetic material into a **hierarchy of populations** was considered, much discussed, and crystallized (Libby 1973). Basically it accommodated the trade-off between large single-generation genetic change achieved through stringent selection of only a few top-ranked trees to be parents of the entire next generation, on the one hand, and genetic diversity that is left largely intact by maintaining much larger breeding populations with lower selection intensity per generation, on the other. The trade-off is illustrated schematically in Fig. 5.20.

At the top of the proposed hierarchy is the **production population**, typically stringently-selected and then cloned plus trees (which give rise to **deployment populations**). Relatively few stringently-selected tens of clones may serve as replicated parents in seed orchards. The same clones, or perhaps their stringently-selected and cloned next-generation offspring, may be deployed either generally, or (usually later following testing) specifically to different kinds of sites as well-characterised clones.

Underpinning that is the **breeding population**, which may contain a few hundreds of less-intensely-selected individual trees or clones; in it, recurrent cycles of selection and intermating produce cumulative genetic changes over generations.

At the bottom of such a population hierarchy are the **gene resources**, thousands of largely unimproved trees containing almost all of the species' genetic diversity. That is the repository of the programme's foundation genetic diversity, which may be conserved *in situ* as natural populations, in dedicated plantations, or in archives that may be augmented over time by additions from native populations, land races and other breeding programmes not previously sampled and included.

With time, an inclusive concept of a breeding strategy developed. Embracing all aspects of breeding, it involved devising a set of measures that are designed, in conjunction, to ensure near-optimal outcomes, in both the short and long terms, despite the many biological and market uncertainties (cf Shelbourne et al. 1986). As thus conceived, no one measure or feature is to be considered in isolation from the rest of the total “package.” For any one aspect of a strategy various options may exist, but the option chosen may dictate the nature of one or more other features of the strategy, so that it is hopefully fail-safe.

Implementation of tree-breeding strategy is much helped by refining methodologies for estimating genetic parameters and for evaluating selection candidates. Both parameter estimation and candidate selection involved choices of trial sites, and among various field designs and methods for data analyses and then actual selection. Experimental designs were refined to achieve greater operational simplicity yet more precise information, while making allowance for limitations in both computers and data-analysis programmes.

Incomplete-block field designs had been used for large progeny tests in Australia from the 1950s (experience and developments in trial design and data analysis were collated by Williams and Matheson 1994). In sharp contrast, for large progeny trials in New Zealand, the sets-in-replicates (set-in-reps) field design (Schutz and Cockerham 1966) was adapted for testing the progeny of the 588 plus-trees selected in 1968. In that case, the progenies were grouped into essentially random sets of about 30 OP families, to create manageable subunits in the hope (generally realized) that differences in average genetic values among sets would be negligible. A further move was made to non-contiguous plots (Libby and Cockerham 1980). However, assigning one individual per family (or clone) per rep/set block within the sets-in-reps field design allowed smaller experimental subunits (blocks) and more-precise comparisons among selection candidates. That also made large datasets easier to analyse, at least with the then-existing computing facilities. It became common to include in progeny trials or clonal trials some of material that represented alternative seed sources, such as standard mixes of OP families or well-characterised “standard” clones, as repeatable “controls” that were then compared with the candidate progenies or clones both within the trials and among different trials.

With a very large breeding population’s progeny in trials, promising candidate trees were seldom side-by-side for the tree breeder to compare them simultaneously. Furthermore, selection needed to be done for several traits for each candidate tree, with traits such as wood properties not readily observable in the field. Initial selections therefore needed to be based on data records. Adapting developments in animal breeding, Mike Wilcox in New Zealand pioneered the use of index selection in forest trees during the mid-1970s. However, the University of California at Davis’ professor of plant breeding, Bob Allard, emphasized to his students that final selection should always be done by experienced practitioners observing the initially-selected candidates in the field. Among other things, those practitioners could see and then include in their final selection decisions unusually favourable expression of traits that had not been included in the computer's selection index (Allard 1960). Such field checks of computer-selected trees were duly made with radiata. They often eliminated individuals or clones with drawbacks that were not included in the index calculation.

Genotype-by-site interactions, and the possible need to create regional subdivisions of breeding programmes, remained a concern at FRI. It was addressed by Shelbourne (1972) and by the methodology developed by Burdon (1977, 1979) in the 1970s for both analyzing data and accommodating interactions in selection. In New Zealand, interactions involving changes in ranking of candidates for individual traits remained surprisingly minor. An exception was in performance on phosphorus-deficient clays compared with elsewhere, but even those interactions did not necessarily call for regionalized breeding (Johnson and Burdon 1990). In Australia, however, important genotype-by-site interactions proved prevalent, but without obvious patterns with respect to widely diverse climates and soil (Matheson and Raymond 1984), although the effects high fertility of some ex-pasture sites on tree form were clearly a source of difficulty for deployment decisions (Horne 1988; Lavery 1988).

In developing breeding strategy for radiata, continuing interactions with overseas personnel was important. Prominent among the influences and collaborators in Australia and New Zealand were Libby of University of California Berkeley, Namkoong of the US Forest Service who was stationed at North Carolina State University, and Hans van Buijtenen of Texas A and M University. In Chile, Zobel played a key initial role, followed by input from Burdon.

5.5.4 Quantitative Genetic Architecture

Intensive breeding of radiata had begun with very little definite knowledge of either the patterns of variation or of the inheritance of important traits among and within its populations. The first systematic comparison of radiata from the entire natural range of the species was the "Genetic Survey" experiment initiated by Martin Bannister and followed through observations and analyses by Burdon (Burdon 1992; Burdon et al. 1992a). That experiment, however, both depended and built on a study by Margot Forde during 1959–1961 of *in-situ* variation in the three Californian populations (Forde 1964). For that study, she had made essentially random cone collections from ecologically representative sites, and those cones supplied the seed for the mainland population samples in the Genetic Survey. Visits by Bannister and Libby in 1964 to the other two native populations, on the islands, completed cone collection from natural populations for the Genetic Survey, supplementing an earlier collection by Dr Reid Moran on Guadalupe Island and collecting afresh on Cedros Island (Libby et al. 1968). For experimental controls, cones of near-random tree samples were taken from two regional

New Zealand land-race populations; one was near Nelson in northern South Island, and the other in Kaingaroa Forest in central North Island.

Planting was done during 1964–1967 in Kaingaroa Forest, New Zealand, on two contrasting sites, one being markedly warmer, somewhat more fertile and less exposed than the other. The basic structure was 50 OP progenies of each of the five natural populations and two New Zealand ones, with some variations in order to accommodate delays in acquiring some seed. A clonally replicated component was added to the 1967 plantings for providing additional genetic information. The experiment was supplemented by three small provenance trials elsewhere in New Zealand using spare planting stock of the same natural populations.

The field design contained a pioneering adaptation of a field design (Libby and Cockerham 1980) intended to allow a series of two systematic 50% thinnings, while leaving equal numbers of each of the 350 progenies).

The FRI Genetic Survey experiment, however, had been preceded by two earlier radiata provenance trials and stimulated a third. One, near Canberra in Australia and planted mainly in 1950, compared samples of the three Californian mainland populations (Fielding 1961a). It surprisingly showed the Cambria population to be the least adapted to that part of Australia, which had seemed more similar to the Cambria environment than to that of the two more-northern populations. The second, established in 1955 on two New Zealand sites (Shelbourne et al. 1979), included only two bulk seedlots from Monterey, one such seedlot from Cambria, and two New Zealand single-parent OP progenies. Limited though it was, it provided a helpful complement to the Genetic Survey experiment.

Following on Forde's study and with her help, cuttings were collected in 1962 from 12 naturally-established randomly-located seedlings in each of 12 ecologically-contrasting sites in each of the three mainland populations. These cuttings were subsequently rooted (Libby and Conkle 1966), with four per clone used to establish two genetic-conservation *cum* breeding archives near Berkeley in 1963, whence a fresh cycle of cuttings were planted in northern California in a clonal genetic-architecture trial in 1970. The archive at the University of California's Russell Reserve, in Lafayette, CA, still existed in 2014, but the other was removed to make way for corn-genetics experiments in 2010. Following damage from a hard freeze (Hood and Libby 1980), a washed-out bridge, an outbreak of dothistroma needle blight and then a western gall rust epidemic on radiata in California, the cloned genetic-architecture trial was abandoned after assessments up till 1978 (Guinon et al. 1982).

5.5.4.1 Population Comparisons and Action Taken

Differences among the population samples in the Genetic Survey plantings became evident from very early on (Burdon and Bannister 1973; Burdon 1992; Burdon et al. 1992b) (Table 5.4), reinforcing some of the earlier findings in Australia by Fielding

Table 5.4 Comparisons among native provenances for selected traits (After Burdon 2001)

Trait/Date of information	Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Growth potential	+	+	+	−	− −
Ease of transplanting	+	◦	−	+(+)	− −
Stem straightness	−	−	◦	++	◦
Corewood density	−	−	−(−)	++	++
Resistance to/tolerance of					
Abiotic factors					
Frost	++	+	−	◦*	− −
B deficiency	+	+	+	− −	− −
P deficiency (1997)	−	++	++	•	•
Soil salinity (1982)	◦	+	++	− −	−
Drought (1995)	− −	−	◦?	+	++
Snow damage (1994)	++	(−)	− −	•	•
Fungal diseases					
Dothistroma blight	++	++	− −	◦	− −
Cyclaneusma needle cast	+	++	− −	◦	− −
Diplodia dieback	++	++	− −	− −	•
Phytophthora root (1984)	− −	+	++	•	•
Western gall rust (1986)	◦	− −	− −	++	+
Animal pests					
Deer/rabbit browse	◦	◦	◦	−	+
Pine woolly aphid	+	+	−	− −	+

*Resistance to winter cold evidently superior

Pluses denote superiority relative to average, minuses inferiority, ◦ roughly average, • no convincing data. Entries based on first substantial published report, in 1973, unless later date stated

(1961a, b). Young seedlings and (later) saplings from the two island populations proved to be distinctive from each other in both appearance and very early growth rates, being similar mostly in having their mature needles typically in pairs rather than threes. Evidently lacking a history of adaptation to frequent light fires (Stephens and Libby 2006), island-population seedlings take much longer to develop the thick, fissured, fire-resistant bark on the lower bole characteristic of mainland, and particularly Monterey, seedling-origin trees; in this and some other respects, adolescent seedlings from the islands resemble grafts or cuttings derived from mature trees of the mainland and land-race populations. The Guadalupe samples were appreciably slower growing than those from the mainland populations, due in part, but only in part (S. Kennedy and C.B. Low unpubl.), to those open-pollinated families having greater levels of inbreeding (Burdon and Bannister 1973; Moran et al. 1988a); their greater inbreeding was doubtless as a result of few nearby pollen parents in Guadalupe's linear relict native population, with those few neighbours mostly living near the ridgeline at right angles to the prevailing wind. Seedlings from Cedros Island, despite less inbreeding, were initially by far the slowest-growing of the five native-population samples. Interestingly, these growth differences were not exhibited in early inter-population hybrids between island- and mainland-origin parents. Browsing animals in New Zealand, while preferring Guadalupe seedlings, tended to shun Cedros seedlings, a contrast in palatability that fitted with the biotic situations on the two islands—Cedros Island has long had a small deer species, in contrast to the historic lack of browsing mammals on Guadalupe Island. Seedlings from both island populations, however, were more prone to suffering from boron deficiency than those from the three mainland populations.

Differences in growth potential among the mainland populations (reflected in growth rates without disease or adverse soil conditions) were not evident. Many other trait differences among mainland populations are less compared with corresponding differences between mainland and island populations and between the two island populations. The mainland populations samples, however, differed markedly in average cone size and seed weight, Cambria having the largest and Monterey the smallest. There were subtle differences in several elements of young trees' appearance, allowing an experienced observer to assign almost every individual to a population on appearance alone. Cambria, however, is the most distinctive mainland populations at various ages, and differences in appearance between Año Nuevo and Monterey were the least obvious. In New Zealand trials, Cambria trees have been much more susceptible to needle-cast diseases (cf Ades and Simpson 1997) and to shoot dieback attributed to *D. pinea*.

An interesting feature is variation among provenances in persistence of juvenile characteristics, which was first expressed clearly in how quickly green apical tufts gave way to brown, sealed buds. Among the mainland provenances, Cambria-origin trees maintain juvenility the longest, followed by Monterey and then Año Nuevo, with Guadalupe showing the fastest acquisition of adult characteristics. Cedros was similar to Año Nuevo in the rate of this phase change, although slower growth of Cedros made rigorous comparison difficult. These provenance differences in rate of phase change, however, have implications for resistance to diseases that tend to affect trees mainly in either the juvenile or the adult phase. This was borne out in provenance comparisons of resistance to western gall rust, which affects juvenile radiata, provenance differences in susceptibility reflecting comparative persistence of juvenility (Old et al. 1986).

The cloned genetic-architecture trial in northern California revealed differences among mainland populations in frost tolerance, with Año Nuevo the most tolerant, and in susceptibilities to animal damage (Hood and Libby 1980). The among-population differences in growth potential were negligible, although the Cambria sample became less thrifty with time (Guinon et al. 1982). These results roughly paralleled those from the New Zealand Genetic Survey experiment.

All populations, however, showed strong tree-to-tree variability in traits such as cone size and shape, and branching pattern, the comparative importance of the genetic and environmental components of tree-to-tree variation depending on the trait. Thus, despite some substantial differences among population averages, there was much overlap in variation for most observed traits. All told, the patterns of variation observed among the populations were complex and multidimensional, such that the pattern of resemblances between pairs of populations differed according to the trait(s) considered.

By 1983 it had become clear that not only were all five native populations members of the radiata species, but that each is different from the other four in many distinguishing and important traits (Table 5.4). This in turn supported the theory that radiata had long existed as a number of small migrating populations, rather than the current populations being survivors of a much larger continuous population (Millar 1999). This had implications as well for identifying the contributions of individual native populations in founding the land races developing in their new host countries. It had also became increasingly clear that the two sampled and analysed New Zealand land-races in the Genetic Survey experiment New Zealand most resembled the Año Nuevo population sample (in the Kaingaroa land race), or some combination of parents from Año Nuevo and Monterey (in the Nelson land race). Those two land-race samples were also proving to be clearly the best-adapted, in terms of overall survival, early growth and health, to the specific environments of the several provenance and genetic-architecture trials in New Zealand (NZ) and Australia. They were followed by the Año Nuevo and Monterey samples.

Independent evidence, from turpentine analyses, also indicated that the Kaingaroa land-race sample (from central North Island, NZ) had originated predominantly from Año Nuevo parents (Bannister 1962); and further, that this sample was broadly representative of radiata in the whole Kaingaroa Forest (Blight et al. 1964). Thus the Año Nuevo population was heavily over-represented in the Kaingaroa land-race ancestry, especially in relation to the relative size of the area that population occupies in California. The Nelson land-race sample (from northern South Island, NZ) later appeared to have a greater proportion of Monterey-origin ancestry, close to 50% (Burdon 1992). In Australia, land-race samples were deemed, on the basis of isozyme results (Moran and Bell 1987) to have come from similar ancestry to that of the NZ samples; but evidence of the proportions from Monterey and Año Nuevo was weak. There was no evidence, historical, circumstantial, biochemical or observational, of any contributions to any NZ or Australian land races from the Cambria or two island populations.

Notably, the two land-race samples all grew appreciably faster, by ca 10% in average height, in the Genetic Survey experiment than any of the five native-population samples. This growth difference was probably attributable, at least in part, to the large plantations from which the land races were sampled not being subject to “neighbourhood inbreeding.” Such inbreeding no doubt occurred to some degree in the natural stands, due to their population structures whereby near neighbours tended to be relatives. Also, the two New Zealand land-race samples exhibited substantially better bole form than did the samples of their two native progenitor populations. That commercially-important difference is likely due to their divergent histories, since the mid-19th century, of mildly eugenic silviculture in the evolution of New Zealand land races and dysgenic selective logging in the mainland native populations, particularly in the Monterey Peninsula part of the Monterey population. Interestingly, the Guadalupe population, with no historic or current evidence of human management, exhibited straighter stems than did the two land-race samples in those trials.

The pre-1983 provenance comparisons in New Zealand were mainly confined to one region, namely the volcanic soils of the Kaingaroa Forest in central North Island. However, there was some additional evidence (Shelbourne et al. 1979) that suggested that infusion of genes from additional Monterey-population parents into future breeds or clones could help confer better adaptation to some other New Zealand environments, or even to future circumstances arising in New Zealand.

In the light of the latest information then available, an expedition was mounted in 1978 to collect additional OP seeds, afresh and systematically, from better-than-average parents in all the five native populations (Eldridge 1978). Various factors drove the decision. It was by then clear that at least some land-race stocks in Australia and New Zealand had been founded by seeds acquired from a only small portion of the species' natural range. Even from the identified two founding populations, their contributed genetic base was probably unbalanced geographically; furthermore, the numbers of their founder parents were unknown and possibly small. There is some circumstantial historic evidence that many or even most of the seeds shipped to New Zealand to create the early radiata plantings were gathered from trees felled to supply fuel for rendering whale oil by shore-whalers, known to then be operating from the coasts of both the Monterey and Año Nuevo populations. Seeds from parents that might have been more tolerant of the soil conditions, higher and/or lower temperatures, less fog, and other features of sites further inland, could well have been under-represented or even unrepresented in founding the existing land races. Nowhere in New Zealand, Australia, Chile, South Africa, California or any other country had the various provenances, particularly samples of their sub-populations, been tested on the wide range of potential radiata sites that would clearly reveal genotypes with such special adaptations.

There was an option of making controlled crosses among parents of known origins in the then-available provenance trials and archives in New Zealand and Australia, in order to acquire pedigreed pure-population seeds for additional trials and to maintain those native populations *ex situ* for future breeding. That would have assured future pedigree-known pure-population status, in contrast to the seeds compromised by pollen contamination from the widespread radiata plantations if OP families from existing and future provenance trials and archives were used instead. Moreover, in the provenance collections for the Genetic Survey experiment, cones had been carefully collected from essentially random parents, and a new collection could concentrate on parents with better phenotypes. Furthermore, it was decided by the leadership in Australia that a new collecting expedition could expand radiata's genetic resources available for breeding and additional trials, making good the incomplete and patchy representation of the natural range of the species in land-race stocks and offering possible advantages in site tolerances, bole form, disease resistance and wood density. In addition, during the collecting, members of the expedition could observe and learn more about the different ecological characteristics of the native stands being sampled. Meanwhile, the Guadalupe population was under imminent threat of extinction, due to the hungry goats, while much attrition was occurring in New Zealand's *ex-situ* Cedros plantings in trials and archives.

The new 1978 collection was planned to favour parent trees, in terms of size, health and bole form, so few of them if any would have been included in the earlier quasi-random collection, except on Guadalupe Island.

A major event for radiata's future domestication, the collecting expedition was not a budgeted part of operational breeding in the 1970s. Instead, it was done by a joint Australian–New Zealand expedition, operating with local assistance in California and Mexico, and additional funding from the US National Science Foundation, FAO and several California Christmas-tree growers. The California growers financially supported and partly staffed the expedition's collecting trips to the two Mexican islands, as then-ongoing research (Old et al. 1986) was showing the island populations to be much more resistant to the western-gall-rust epidemic then devastating the extensive radiata Christmas-tree farms in California.

With few exceptions, large numbers of seeds were successfully collected from each of around 520 trees in the mainland populations and in lesser quantities from 99 trees in the island populations (Eldridge pers. comm. to WJL 1997). Those seeds were shared mainly by Australia, New Zealand and, in the case of the island collections, Mexico, with small amounts going to other countries, including Chile (Jayawickrama and Balocchi 1993), South Africa (Falkenhagen 1991) and Greece (Matziris 1995). In both New Zealand and Australia large networks of provenance trials were quickly established, especially of mainland material (Eldridge pers. comm. to WJL 1997), in order to obtain comprehensive profiles of the populations' and sub-populations' site tolerances. In addition, substantial gene-resource plantings were made in both New Zealand and Australia.

5.5.4.2 Within-Population Variation

Observed variation in putatively adaptive traits among the samples from different sites with contrasting ecological conditions within each natural population was, as of 1983, generally minor in the various provenance-trial environments in New Zealand and Australia. That was particularly surprising in the case of the samples from the large Monterey population, where there are major among-site differences in soil type, elevation, fog-days, maximum and minimum temperatures, aspect, and distance from salt-laden winds. Accepting this early evidence, the FRI breeders' main interest continued to centre upon general tree-to-tree variation in several growth-and-form traits, their coefficients of variation (standard deviations divided by means), narrow-sense (additive) heritabilities, and genetic correlations among traits.

Analyses of data, by trait and by population sample, from the two large Genetic Survey trials provided support for the following findings from small earlier trials, namely that traits of interest differ widely in both coefficients of variation (CVs) and narrow-sense heritabilities (Burdon 1992) (Table 5.5). Growth traits, especially

Table 5.5 General importance and indicative information on variability and inheritance of selected individual traits in radiata, as basically known by 1983 but often confirmed later (Mainly after Burdon 2001)

Trait	Economic importance	Status[a]	Coefficient of variation (%)[b]	Heritability	Importance of[c]	
					Non-additive gene effects	Genotype-site interaction[d]
Height growth	High	No	12	~0.2	••	••
Diameter at breast height	Very high	Sel	15	~0.2	•••	•••
Stem volume	Very high	BG	30	~0.2	•••	•••
Straightness	High	BG	–	0.4	••	••
Branching frequency	High indirect	Sel	20–30	0.45	◦	•
Branch size	High	Inc	–	0.2	•	•
Branch angle	High	Inc	–	<0.2	•	•
Wood density	Can be high	Sp				
Cores/discs	”	Sp	7–8	≥0.6	◦	◦
Indirect	”	Sel	–	0.3–0.4	◦	◦
Fibre length	Now low	No	10	>0.5	◦?	◦?
Grain spirality	Significant	Sp	>50	>0.5	?	•••
Cone dimensions	None	No	12–18	>0.5	◦?	•
Cone volume/ seed weight	None	No	20–35	>0.5	◦?	•
Resistance to						
Dothistroma	Locally high	Sp	–	0.3	◦	◦
Cyclaneusma	Variable	Sp	–	0.1–0.35	◦	◦
Phytophthora	Locally high	Sp	–	0.8	◦?	◦?
Frost	Limited	No	–	<0.2	?	?
Wind damage	Variable	No	–	0.05	?	?
Leader dieback	Variable	Inc	–	0.05	?	?

[a] BG denotes key breeding-goal trait; Sel – Key selection trait for indirect breeding-goal selection; Inc – often addressed incidentally by selection trait(s); - Sp – addressed in specific situations; No – not generally addressed in breeding

[b] Tree-to-tree, if there is a meaningful measure

[c] ◦Denotes almost always unimportant, to ••• denoting can be very important

[d] Involving rank changes among environments

bole diameters at standard “breast height” (1.4 m), tended to show high CVs (often 15–20%) but fairly low heritabilities (typically ~0.2). In contrast, wood density showed a much lower CV (~8%) but much higher heritabilities (~0.5–0.7). Internode length (or its approximate inverse, frequency of branch clusters) proved not only unusually variable (CV ~20–30%), but also strongly heritable (~0.5) if measured accurately. Stem straightness, with indeterminate CV, showed lowish observed heritability (0.1–0.3) partly because of the need for visual ratings. Heritability of forking, which can be highly dependent on presence or absence of leader-damaging agents such as brush-tailed possums or diplodia dieback, was estimated as very low (0.05–0.1). These different estimates were generally consistent for each trait analysed across all native population samples, land-race samples, and even across estimates from hierarchies of plus-tree offspring (except where intensive selection had already occurred for branch-cluster frequency). As well as exhibiting low heritabilities, even within sites, bole diameter was later shown to show relatively high genotype-by-environment interactions and non-additive gene effects (Sect. 6.7.2.3). Of largely academic and taxonomic interest, cone traits were very variable among trees and evidently highly heritable (Burdon 1992).

Taking account of some additional trials (e.g. Burdon 1971), diameter growth showed important genotype-by-site interactions, especially when the trials were replicated across contrasting phosphate-deficient and nutritionally balanced sites. Some strong genetic intercorrelations were emerging, long "internodes" between branch clusters tending to be associated with larger, steeper-angled branches, more frequent forking and ramicorn branches, and somewhat more bole crookedness. The cloned genetic-architecture study in California (Guinon et al. 1982) showed broad-sense heritabilities there of around 0.15–0.2 for diameter growth and some tree-form traits, but much lower for incidence of forking (~0.05).

For various between-trait genetic correlations, analyses of data from the Genetic Survey generally supported and refined previous weak estimates (Burdon 1992, Table 3). A set of favourable genetic correlations among branch-cluster frequency (viewing high as desirable), early growth rate, bole straightness and freedom from forking were confirmed. So, too, was the adverse genetic correlation between growth rate and wood density. Looking at different growth-rate variables, however, the story is more complicated (Burdon and Low 1992). The genetic correlation between height growth and wood density was less adverse than that between bole diameter and wood density. In practical terms, that means that trees with a tall, slender growth habit tend to have greater wood density than ones with a short, fat growth habit.

Interestingly, genetic intercorrelations among most traits, as with heritabilities, were generally consistent among the different population samples. That suggested that those correlations are at least partly due to pleiotropy, with at least some of the genes affecting both of the genetically-correlated traits. Where pleiotropy generates adverse genetic correlations, breeders are faced with unavoidable constraints on the amount of desired genetic change that is simultaneously obtainable for such adversely-correlated traits. However, all is not lost when two important but adversely-correlated traits are identified. In the usual case, where the genetic correlation is <1.00, breeders can clonally test and select "correlation breakers" which show some departure from the adverse relationship because of pleiotropy between traits being less than 100%. Trees with favourable combinations of genes affecting only one or the other of adversely correlated traits can be identified, accumulated by breeding (more difficult), and clonally deployed (Libby and Rauter 1984).

5.5.5 Breeding and Seed-Orchard Technology

Problems with seed orchards abounded, including delayed graft incompatibility, poor production of **female strobili**^{G}, abortion of conelets after pollination, and depredations by various animal pests.

For reasons still unknown, incidence of delayed graft incompatibility varied a lot with site. This incompatibility typically killed many grafts about 10 years after planting, when those ramets were just coming into full seed production. This would frequently be preceded by one or two years of super-abundant "stress crops" of both pollen and female strobili, followed by decline and then death of the tree as translocation of water and nutrients was ceasing at the failing graft union. Quests were conducted for rootstocks with better and more-general graft compatibility, with some success with Douglas-fir. But no "universal recipient" rootstock for radiata was found that was graft-compatible with a wide range of parent scions. An alternative solution was to root cuttings that were at a maturation state near or at sexual competence, usefully aided by "ringbarking" twigs on the donor tree (a graft prior to onset of incompatibility) several months before their removal as cuttings. It was a laborious solution. The efficiency of this option was somewhat improved by hedging late-adolescent ramets of desired parents that were in clonal archives, to produce the numbers of late-adolescent or mature cuttings required for planting in new or expanded seed orchards.

The rapid height growth of radiata grafts and cuttings in the seed orchards made managing those parents and collecting their cones difficult (Fig. 5.21). Also, large differences among the parent clones in fecundity, especially in viable conelet production but also in pollen production, were soon evident. This meant that the "effective number" of parent clones producing the wind-pollinated seeds in an

Fig. 5.21 Pollarding trial in Gwavas Seed Orchard, Hawke's Bay, New Zealand. Aimed at preventing grafts becoming unmanageably tall, this practice reduced seed yields unacceptably. Recourse was made to climbing and/or use of hydraulic hoists

orchard, a measure of genetic diversity in the offspring generation, was often far less than the "census number" of different clones in the orchard. Once recognized, this "effective number" could be brought to a desired level by adjusting the ratios of the different clones in the orchard, favouring the less-fecund in order to boost their representation in seed parentage.

Bark beetles, if sufficiently plentiful, could girdle recently planted grafts, although this was a minor and temporary problem. Birds, particularly chaffinches, ate strobili-containing buds. In New Zealand, brush tailed possums would eat pollen catkins, and subsequently ate immature seed cones. And in Australia, cockatoos all too frequently ripped open nearly-mature cones, playfully and annoyingly ate only one seed, and wantonly discarded the rest. In general these problems could be dealt with, but often that took much time and effort.

In New Zealand, these problems with managing seed orchards spurred much research at FRI, led by Geoff Sweet on several fronts. Graft incompatibility was researched, helped by Bob Kellison during a year-long sabbatical visit from North Carolina State, trying remedies used for loblolly pine, without achieving any clear solution. However, enhanced initiation of both male and female strobili proved possible with the application of gibberellins, specifically GA 4/7 (Ross et al. 1984). Although the most responsive clones were the ones that already flowered best, thus maintaining or increasing fecundity differences, this became and has remained operational practice. Various crown-shaping regimes were tried, analogous to pruning fruit trees, in order to achieve less expensive controlled pollination and more convenient cone collection (e.g. Sweet and Krugman 1978). The FRI orchard-pruning regimes were subsequently adopted in Western Australia, under the leadership of Trevor Butcher, and modified as HAPSOs (Hedged Artificially Pollinated Seed Orchards; Wu et al. 2007) (Fig. 5.22).

Fig. 5.22 Hedged Artificially Pollinated Seed Orchard (HAPSO) in Western Australia, Pollen being blown onto receptive conelets with the help of an air compressor. Further control of pollination was achieved by spraying maleic hydrazide to suppress pollen catkin growth on recipient ramets (Photo T. Butcher)

Given the problems with clonal seed orchards, in 1977 the proposal was made by Burdon (unpubl.) in New Zealand to establish ESSOs (Extensive Seedling Seed Orchards). Controlled crosses could be made among a large number, say 50, of top-ranked clones. As needed, the resulting seedlings could be multiplied in nurseries by rooting several juvenile cuttings from each of them. The resulting cuttings could then be planted in areas managed to produce both good quality logs and seed. While expected genetic gain would be less than from a clonal seed orchard, this was seen as a low-cost back-up for the clonal seed orchards. Proof-of-concept plantings were duly made, but they never produced harvested seed, partly because demand for genetically improved seed was being increasingly met by mature-clone orchards, and partly because possums in uncontrolled numbers were allowed to destroy almost all the growing conelets.

Despite the various problems with early clonal seed orchards, they eventually succeeded in providing abundant seed with major genetic improvement in growth and form. Indeed, it was soon after 1983 that New Zealand's seed orchards were able to meet the radiata planting needs for the entire country (Vincent 1986). Not only that, it was then hoped to export considerable quantities of their seed, of which the progeny of at least some of the parent clones were known to perform well in Australia.

Ironically, the findings of much good and painstaking research were overridden by the realization that correct choice of orchard site could avoid several of the main seed-orchard problems. The early preoccupation with pollen isolation (Fig. 5.23) often led to choosing inherently unsuitable sites for seed production, without always achieving effective isolation. The present-day ideal for a New Zealand radiata seed orchard is a sunny, largely frost-free site, with modest but sufficient rainfall and good drainage, located close to the sea. This important latter

Fig. 5.23 View of Tallaganda Seed Orchard, in NSW near Canberra in an isolated montane location surrounded by eucalypt forests. Such sites were used for a number of seed orchards in NSW, ACT and Victoria, but seed yields were poor or modest compared with those on more maritime sites (Pederick and Brown 1976) (Photo AGB)

criterion was suggested by profuse cone production very near the coast in both planted and natural stands in California, and noted in planted coastal radiata pines in New Zealand. It then was observed to be the case in the already established Amberley seed orchard, located 1–2 km inland from New Zealand's east coast, 20–30 m above sea level about 40 km north of Christchurch. There, the ramets did not grow unduly tall, delayed graft incompatibility was not seriously troublesome, conelet production was early and plentiful, clonal variation in fecundity was less, conelet abortion was minor, and the number of filled seeds per cone was high. Indeed, this orchard was soon seen as the benchmark for orchard performance. The Chilean breeding programme, in particular, benefited greatly from knowledge of the site characteristics and orchard performance at Amberley.

5.5.6 Mass Propagation by Vegetative Means

In the early stages of active breeding of radiata, vegetative propagation in the form of grafting had been widely used as a breeding tool to establish clonal archives and thence clonal seed orchards. When graft incompatibility had not been effectively overcome by around 1970, research attention was increasingly refocused on techniques for using sexually-competent cuttings for establishing additional orchard areas (Box 5.3).

Box 5.3 Applications of Vegetative Propagation

Vegetative propagation by grafting was originally used operationally with radiata for establishing clonal archives as a preliminary to establishing seed orchards. Grafts behave like the tops of the mature trees from which they are usually taken, and in radiata are subject to troublesome delayed incompatibility. An alternative, which works very well starting with young seedlings, is to set and root cuttings, but in-vitro methods have since been developed for vegetative propagation of radiata. Vegetative propagation from an individual produces ramets of a clone that are genetically identical to each other, ensuring faithful reproduction of a genotype, but generating no new genetic variation.

Small quantities of seed can be "extended" by vegetative multiplication, typically to produce large numbers of planting stock from pilot quantities of seed from the latest and very best clonal selections. This is widely done operationally, with the help of measures that delay maturation, maturation being a process whereby cuttings become progressively harder to root as the trees become bigger and older.

However, using vegetative propagation on a massive scale, as a tool to deliver genetically improved planting stock to radiata plantations, was first attempted in the early 1960s by J.M. Fielding, trying to build on propagation research in Australia and New Zealand during the 1930s. Importantly, Fielding hoped to achieve thereby a bonus in tree form by avoiding the untidy juvenile growth habit of seedlings. Large-scale propagation of post-juvenile material, however, soon proved impracticable, and mass vegetative propagation for producing plantations took another two decades to attain operational feasibility.

Prior to the 1970s, for "good" cuttings, breeders and propagators wanted shoot terminals that were growing in full light, thus producing cuttings that were in good physiological condition. In closed-canopy stands, those were branch terminals in the upper crown. That seemed *such* a good idea at the time, yet it was brutally counterproductive for rooting such cuttings to produce plenty of cheap and vigorous planting stock. What was not generally realized then was that successful rooting and good growth of cuttings depended on the material being in both good physiological condition and in an early maturation state. By the mid-1960s enough was known from propagation studies with radiata, and from similar studies of other conifers elsewhere, to discourage breeders from trying to mass-propagate plus trees nearing rotation age as cuttings (Fig. 5.24). Instead, they tried working with cuttings from promising seedling-origin trees at adolescent maturation states, namely trees young enough for their cuttings to root readily, yet large enough to show bole form of at least their butt logs, and old enough to give some confidence in evaluations of their early health, growth rate and some other important traits including wood density. That approach failed because, by the time the better performers among those clones could be confidently identified in clonal tests, the ortets and even their ramets in test had become too mature to repropagate at acceptable cost (Wilcox et al. 1976).

This problem was increasingly understood (Sweet 1973; Tufuor 1973; Greenwood and Hutchison 1993) as due largely to "meristem maturation," which for a time was misleadingly called "physiological ageing." Acceptance by many

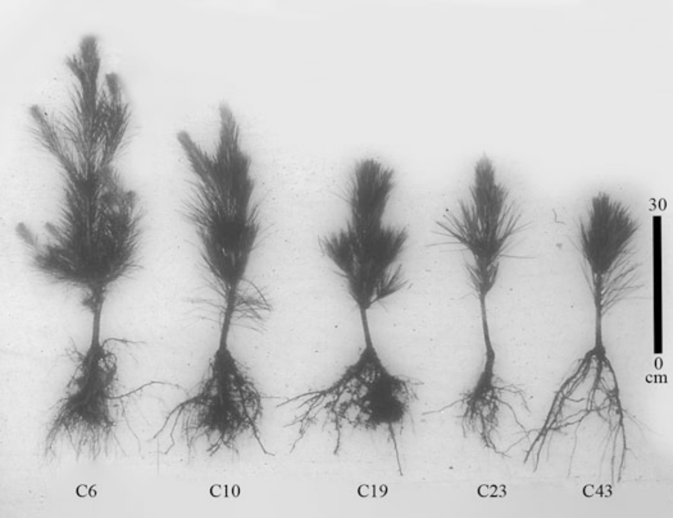


Fig. 5.24 Cuttings taken from trees aged 6, 10, 19, 23 and 43 years, two years after setting and before planting out. These illustrate the progressive decline in vigour which is matched by increasing difficulty of rooting

of that latter term had led to generally ineffective attempts at physiological solutions, such as changes in nutrition or applications of auxins and other plant-growth regulators. Furthermore, it was increasingly appreciated that a tree does not have all its meristems at the same maturation state at the same time (Tufuor 1973). Indeed, the most-mature meristems are in or near the terminal bud, while meristems lower on the tree are at various less-mature maturation states. Vigorous upper shoots on a sizeable tree may be in splendid condition, but they are the most mature and thus very difficult to root as cuttings.

Carefully observing seedling-origin trees at different chronological ages led to better understandings of the maturation process. A very young seedling of radiata looks greatly different from terminal shoots on a mature tree. Young seedlings have soft, paleish-green juvenile foliage dominated by primary needles. That juvenile appearance changes as the seedling grows larger, and genetically-programmed changes in its meristems' DNA-regulation progress occur. Secondary needles grouped mainly in threes (or twos in the island populations) appear as dormant short shoots (fascicles), and brown, sealed buds appear instead of green tufts of foliage at shoot tips. Other changes occur with time as the sapling gets even older and taller. Among those changes, the branching pattern becomes more regular, producing a "tidier" growth habit, pollen- and cone production begin as sexual competence develops, and the lateral meristems (cambia) produce longer and coarser tracheids. So increasing difficulty of rooting cuttings is but one of a whole suite of changes accompanying increasing maturation.

Later, carefully observing replicate cuttings produced from different parts of the same donor tree helped sort out changes in those various traits caused by meristem maturation from more ephemeral changes that could be influenced by altering the environment and/or physiology of the propagule. In general, it was becoming clear that the lower on the tree a cutting was taken, the less mature its maturation state (Tufuor 1973. But, for example, cuttings from the shady side of the tree did root differently from cuttings taken from the same height on the sunny side of the same tree. That and similar results indicated that developmental genetics, ambient environment and some changes in physiology imposed by the propagator all played a part. But the cutting's maturation state seemed most important for efficiently rooting it, and it was the most difficult to alter.

A solution was suggested by observations of tree species (such as redwood) that can produce sprouts or coppice shoots from stumps after felling. Even if the logged trees were old and fully mature, such stump sprouts have nearly the same juvenile characteristics as seedlings of the same height as the stumps. Furthermore, the tops of such fresh stump sprouts seem be at late-juvenile or early-adolescent maturation states. For radiata, a promising solution was to keep seedlings intended to serve as cutting-donors hedged close to the ground (Libby et al. 1972), effectively anticipating scientific findings on maturation state (Bolstad and Libby 1982). Year after year, the regrowth shoots would look fairly juvenile and root almost as readily as cuttings from first-year seedlings. While such hedges could not be maintained in a near-juvenile state indefinitely, this approach had enormous practical applications by the 1990s.

It may be noted that differing maturation states can contribute substantially to **C-effects**$^{\mathbf{G}}$ (or c-effects) within clones (Burdon and Shelbourne 1974), which mimic unwanted genetic variation and represent a form of **epigenetic**$^{\mathbf{G}}$ effects.

In parallel with ongoing research on rooting radiata cuttings for planting stock, research began at FRI on its propagation in the laboratory using tissue-culture to produce "test tube babies." This was a new avenue of propagation technology, aimed at being able to apply a technology to radiata that was already being developed for a number of plant and animal species, including humans. During the 1970s, under Roger Cameron and then Geoff Sweet at the New Zealand FRI, Kathy Horgan pioneered and led the development of tissue-culture propagation of radiata, operational use of which was vigorously pursued after 1983.

By 1969, the tree breeders at FRI had identified two strategic foci: (1) acquiring and managing radiata's genetic diversity for short- and long-term genetic changes; and (2) researching a short-term operational goal of developing vegetative propagation, particularly rooting and raising mature-phase cuttings so as to make clonal seed orchards work reliably. Developing moderately large-scale vegetative propagation of planting stock for those orchards soon involved an increased emphasis on nursery research, to more reliably grow such stock in a field-ready state. Meanwhile and in parallel, research on growing very large numbers of more robust field-ready seedlings of radiata, destined for large-scale plantations during a broadened planting-time window, had largely come to fruition.

Balanced against the bad effects of maturation on propagability and early growth rate were the prospective benefits of planting late-juvenile and adolescent cuttings (and later, tissue-culture plantlets) on tree form, and their resistance to such things as toppling in heavy wet soils and to diseases of juvenile radiata. It was with this in mind that in 1982 Bunn established a new research unit at FRI, Propagation and Early Growth (PEG), under Mike Menzies (Sect. 5.3.2). It was tasked to address the interplay between available and developing vegetative-propagation techniques and the important differences in growth and bole form developed by various maturation states of radiata cuttings, but even by unrooted cuttings set directly in plantations, and perhaps by plantlets beginning to come from propagation *in vitro*. Of major interest was how maturation of conifers, particularly in radiata, could be effectively and efficiently controlled, and how exactly maturation state affected propagability, growth rate and tree form. Such knowledge would then support more beneficial deployment of radiata propagules at maturation states beyond early-juvenile.

Early efforts to mass propagate cuttings from tree 5–7 years old, while giving promising early results (Fig. 5.25), proved impractical. It emerged that deploying cuttings having 2–3 years' greater initial maturation state, compared to that of seedlings, could substantially benefit tree form (Menzies et al. 1988) and greatly reduce severity of diseases such as western gall rust (Old et al. 1986), without seriously affecting their propagability and early growth (Fig. 5.26). As the promise of bringing "somatic" embryogenesis on line became a longer-term goal, 1980s PEG research nevertheless continued to refine the production of plantlets *in-vitro* by tissue-culture, transitioning the small, delicate plantlets from the conditions inside a culture dish to greenhouse and then to outdoor conditions, growing them in

Fig. 5.25 Tasman Forestry Ltd's oldest stand of cuttings, taken from 7-year-old trees, in June 1986, 16 years after planting. The trees feature good bole form and thin bark, reflecting the age of donor trees and choice of donors with "short-internode" branching pattern; and similarity of habit and cones, a consequence of many of the trees belonging to the same clones

Fig. 5.26 Comparison of seedlings (left) and cuttings taken from 4-year-old trees (right), the latter showing a less bushy, more open crown habit. Ageing of donor trees can improve tree form sooner than it depresses growth rate, but production of cuttings tends to become more expensive as tree form improves

nurseries to become field-ready plantlets, and researching their subsequent growth. Later on, towards 1990, PEG was ready to begin research on somatic embryogenesis, which was aimed at eventually producing field-ready "emblings" and even encapsulated artificial seeds.

Despite the logical links between GTI and PEG, they were for nearly 10 years administratively placed in separate divisions of FRI, a situation that much impeded communication and collaboration toward common goals.

5.5.7 Demonstrating and Quantifying Genetic Changes

Proving, quantifying and financially valuing genetic improvement are important both politically and technically. Politically, this is needed to justify ongoing financial support, not only for continuing the radiata breeding programme but also planned breeding programmes in other species, such as Douglas-fir, cypresses and eucalypts. Technically, several purposes are served. Genetic changes achieved after one or two generations of breeding could be expected to affect harvest yields and some elements of log quality, particularly bole straightness. Information on such effects is needed for planning future harvests and thinking ahead to marketing. Hard data from fair trials of new breeds allows fine-tuning and revision of models predicting future yields and log outturns. Demonstrated genetic changes also have implications for management and silvicultural regimes, and allow knowledge-based changes in initial spacing, in thinning and pruning regimes, and even in future harvest ages.

Some conflicts exist between meeting the political needs and the technical needs, despite both being served by demonstrating genetic changes. Side-by-side plots of genetically improved breeds and unimproved control seedlots (representative of alternative genetic stocks for planting) often showcase dramatic differences and are thus politically effective. However, such paired comparisons tend to be achieved at the expense of the proper, fair experimental replication that is needed to provide reliable data that are convincing to scientists and “hands-on” managers and provide a sound base for future planning.

Early progeny trials typically contained “routine” seedlots, which were generally genetically unimproved seedlings, as “controls.” Typically, the controls performed as had been observed in plantations before, and most of the select progenies duly exhibited improvement of the selected traits, which reassured at least the tree breeders. But in Australia, by the mid-1970s, political pressures were coming for more rigorous demonstration of genetic gains. This prompted such analyses and a preliminary paper given at the 1977 3rd World Consultation on Forest Tree Breeding (Sect. 5.1). That paper reported modest but variable increases in growth rates and straighter boles, based on the rigorous analyses of data from three young trials (age 5½–7 years). Later, at ages 10–12 years, further analyses (Eldridge 1982) indicated that such gains were by then more consistent, and thus more certain. Those later analyses indicated around 20% greater average stem volume and much better tree form in seed-orchard seedlots compared to the controls.

In New Zealand, some of the very early progeny trials, both replicated and unreplicated, showed some OP families with, on average, dramatically straighter stems, lighter and more regular branching, and much less malformation. Such manifest gains in these important tree-form traits fully convinced foresters of the benefits of breeding. Even so, it was deemed appropriate to set up special genetic-gain trials (Burdon et al. 2008), to quantify genetic changes obtainable from select-tree seed collections, seedlots from the various regional seed orchards, and from seedlots designed to simulate the outturns of future seed-orchards, and to predict the performance of future plantations to be established using those genetically-improved seeds.

In 1978 and 1979, two major series of multi-site Genetic Gain trials were established. Each year, two types of trial were planted:

1. "Small plots," using six-tree row-plots, well replicated and incorporating a range of control lots, aimed at giving precise rankings among seedlots. These, however, are prone to competitive effects between adjacent rows of seedlots, thus generally exaggerating growth differences among the seedlots.
2. "Large plots," 6 trees × 6 rows giving 36 trees per plot, with fewer controls and less replication, but designed to better simulate crop-level rather than individual-tree performance. Because the outer rows and columns are so subject to competitive effects of the neighbouring plots, data from only the inner 16 trees were used to give a measure of stand-level performance of each genetic entry.

Those early trials, and subsequent ones, were meant to demonstrate and quantify the genetic gains in traits of interest. Their data could form the bases both for financially evaluating such gains and for more persuasive, honest and effective marketing of genetically improved seed (Vincent 1987), and for projecting the harvest yields (Carson et al. 1999) and possible product-grade outturns of the resulting plantations.

Nurserymen often expected to see genetic improvement showing as better-looking, faster-growing seedlings in their nurseries, only to be disappointed. Instead, it turned out that genetic improvement in radiata starts to be expressed clearly in the field only after about five years. On the other hand, for various reasons the seedlings from seed orchards often made comparatively slow starts, which could be made good into meeting planting-stock specifications by skilled nursery management. Despite this, economic benefits of genetic improvement could and often did accrue from the time of planting onwards. For many plantations, foresters decided that fewer trees needed to be planted per hectare, because less provision had to be made for thinning out malformed trees. Pruning better-formed trees was cheaper and the payoffs from pruning were greater with straighter boles. And, in addition to increases in total stemwood per hectare and various changes in log quality, fewer forked and other malformed trees made for safer logging and less logging waste. Finally, at that time it was believed that genetic improvements would be able to offset the adverse effects on overall crop quality associated with silvicultural regimes designed to reduce effective growing costs by such measures as fertilizer use, heavier thinnings and shorter rotations.

5.6 Summary of Domestication Progress

Booms of new planting of radiata developed in New Zealand and Australia, and the planting boom continued in Chile despite a lull associated with political upheavals. Thus the total area of radiata plantation increased substantially. Intensive tree breeding spread to Chile, where tree breeders were able to take advantage of hard-won experience in Australia and New Zealand.

Comparative financial analyses of alternative silvicultural regimes for radiata in New Zealand led to another major advance in radiata plantation forestry. A key finding was that, in most local conditions, commercial harvesting of thinnings was generally uneconomic, because that reduced the overall profitability of the crop. That led to widespread adoption within New Zealand of the unconventional Direct Sawlog regime, which featured wide early spacing, and early and heavy thinnings coordinated with aggressive pruning of lower branches, but with no harvesting of thinnings. As follow-up, stand-modelling software was being developed to predict log and product outturns from alternative growing regimes on various site categories, an activity that has remained the subject of continuing refinement.

Together with developing the Direct Sawlog regime was the development in New Zealand of silvo-pastoral systems for converting pasture land into radiata plantations. While such systems were used there for converting large areas of pasture into forest plantation, the benefits of grazing for interim financial yields were generally disappointing. Tending systems were also being refined for radiata shelterbelts that could provide high-quality timber.

Increasing awareness of the need to assure continued genetic gains led radiata breeders to develop multi-generation breeding strategies, an important contribution to the relatively new discipline of tree breeding. An immediate result was the expansion of many tree-breeding programmes, often by adding large numbers of fresh selections from land races or natural stands, to supplement breeding lines based on too few plus trees. It also led to elaborate population structuring for the genetic material, to avoid deploying inbred material and to better assure future genetic gains while capturing large immediate gains.

By 1983, seed orchards were delivering genetic gains in almost all the radiata planting stock for New Zealand and South Africa and in much of that for Australia. Some of those gains were already giving financial payoffs by saving some important growing costs. However, some downsides of the combination of genetically improved stock and new silvicultural regimes, in the form of greater than expected declines in the wood quality of the harvested crops, were not yet evident.

Intensive research to improve practices in the nursery and in field establishment produced advances in husbandry which were important both in themselves and for capitalising on radiata's genetic improvement. Thereby, better (less wasteful) use could be made of expensive seeds and their promised genetic gains.

Early findings comparing native provenances of radiata prompted a major fresh round of seed collection in all five of radiata's natural populations. This was mounted by Australia and New Zealand, with support from US agencies and FAO. This was to ensure the availability for breeders of the full range of radiata's natural variability, and recognised its international importance as a resource. The seed was used for establishing numerous provenance trials and a number of gene-resource plantings.

Research on vegetative propagation was vigorously pursued. Some was for improving seed-orchard systems, for which novel options were studied, but orchard siting emerged as a pre-eminent factor. Other propagation research achieved successful mass multiplication of seedlings as nursery cuttings, and *in-vitro* multiplication of seedling embryos into field-fit plantlets. Such multiplication systems offered accelerated capture of genetic gain in the quality of planting stock.

Early attempts to develop clonal forestry with radiata, for better tree form, more genetic gain and crop uniformity, had failed, principally due to the phenomenon of maturation. However, some progress in controlling maturation was achieved by the practice of hedging donor plants for cuttings. The various influences of increasing maturation on propagule performance became better characterised.

Genetic-gain trials began to be planted, to achieve rigorous demonstration of genetic gains and to provide a basis for tracking the expression of genetic gain through the life of the crop.

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