Chapter 7
A Wild Ride, 1998 Onwards

7.1 Introduction

The last chapter covered major developments in radiata's domestication, namely:

- propagation technology, which offered speedier and better targeted capture of genetic gain
- monitoring of genetic gain and systems for guaranteeing genetic quality
- much more focus on genetic improvement of wood properties
- institutional changes, in ownership of forests and in R&D organisations
- mounting of molecular genetics programmes with radiata
- continuing development of decision-aid models for the growers.

This chapter continues with numerous threads to the story. Major threads, however, are

- ongoing institutional changes, in both forest ownership and R&D organisations
- continued and intensified focus on the wood properties, in both research and operational breeding
- periodic biotic alarms
- refinements of predictive and decision-aid models for growth and wood properties in conjunction with advances in remote-sensing technology
- emphasis on molecular genetic research.

The 1997 IUFRO Conference *Genetics of Radiata Pine* (Burdon and Moore 1997), drew together much of the existing literature on the genetics. That meeting and collected proceedings having not been repeated; such literature now tends to be more dispersed. Another factor, however, is the increasingly proprietary nature of genetic information, which tends to delay or even prevent publication of some research results. However, literature reviews of genetic parameter information for wood traits in radiata have become available (Wu et al. 2008; Gapare et al. 2009), as have three historical accounts of breeding radiata in Australia (Wu et al. 2007a;

R. Burdon et al., *Domestication of Radiata Pine*, Forestry Sciences,
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Johnson et al. 2008) and New Zealand (Burdon et al. 2008). Moreover, Mead (2013) recently completed a book *Sustainable management of* Pinus radiata *plantations*.

7.2 Institutional Developments

Institutional changes have continued rapidly, and some have been dramatic (Box 7.1). Not only that, some are still in progress, with their full impacts yet to be felt. Often corporate changes have involved changes not only in forest ownership, but also in ownership of processing plants and in their technology arms. The following paragraphs are not an exhaustive coverage of name and ownership changes and lesser reorganisations within the various institutions involving radiata worldwide, but they are meant to illustrate the trends.

Box 7.1 Institutional Turbulence

The last 20 years or so have been turbulent for many of the institutions involved in the various aspects of growing radiata. This, however, has often been true for corresponding institutions involved in various other major plantation forest species. Ownership of and management of forest have seen major changes, which have often been disruptive. R&D organisations have tended to come under pressure, and one key organisation, CSIRO Forests and Forest Products in Australia, has been fully disbanded. Commitment to conservation and management of gene resources—the back-up genetic variability—has often been manifested more in words than in provision of funding and other resources on the part of industry.

In Australia (Productivity Commission 2008) and New Zealand, there was a general trend for state or national governments to restructure their forest services. The commercial forest estates and their management were segregated into corporatized trading organisations, with management of ecological conservation forests coming under separate agencies. This had already happened in 1987 in New Zealand when the exotic forest plantations, which were very predominantly radiata, were placed within the newly created New Zealand Forestry Corporation (NZIER 2000). In 1993, in Australia, the Victorian Plantations Corporation was similarly created from within Forests Commission, Victoria. In 2001, the South Australian Forestry Corporation was established, with ForestrySA as its trading arm, and it opened a new head office in Mt Gambier in the Green Triangle. In NSW, Australia, the Forestry Commission of New South Wales had changed name to State Forests NSW, with a separate commercial trading arm, but full corporatisation took until 1 January 2013. Such government corporatisation has generally been followed by privatisation: in New Zealand during 1992–1996 (NZIER 2000), in Victoria in 1998 (Anon 1998) and in the Green Triangle region of South

Australia in 2012 (Smith 2012). Similar developments have occurred in Queensland, but have involved only very minor areas of radiata.

The pattern for actual privatisation has been for the governments concerned to retain land title, the sales involving the remaining assets, such as the growing trees, the harvesting rights and some processing plants. In some cases, however, the transfer of assets was subject to covenants relating to land use, existing research plantings including genetic trials and tree-breeding material, or wood-processing activities. In New Zealand, the land titles concerned have generally devolved from government ownership into Maori tribal ownership under the terms of Waitangi Treaty settlements.

7.2.1 *Forest Ownership and Activity*

Forest and associated land ownership continued in a state of flux (cf Burdon and Carson 1999). Indeed, major developments occurred in Australia, New Zealand and South Africa, largely involving new types of forest owner. Changes in controlling forest ownership have brought changes in management, which have often been followed by further changes occasioned by internal corporate reorganisations.

In Australia and New Zealand major buyers of forest estate included **Timber Investment Management Organisations (TIMOs)**, the larger transactions being listed in Table 7.1. Of these TIMOs, Hancock (variously Hancock Forest Management or Hancock Timber Resources Pty Ltd) was largely managing pension funds, while Harvard (as Harvard Management Company) runs a research endowment fund. Pru Timber was basically Canadian, being mainly owned by the Ontario Teachers Pension Fund, but had actually been taken over by Hancock.

Note that these figures do not include short-term double transactions or some subsequent changes of ownership. The TIMOs concerned operate strictly as forestry companies, not as processors, maintaining a widespread trend away from vertical integration of forest growing and wood processing. They have had a two-fold advantage over traditional corporates for running forestry as a business: some tax advantages, and the fact that the investment money comes in as retirement or

Table 7.1 Some TIMO purchases of radiata plantation forest (as cutting rights) (After Horgan 2004)

Year	Where	Seller	Buyer	Radiata (ha)
1998	Australia (Victoria)	Forests Commission	Hancock	170,000
2006	New Zealand (Kinleith Forest)	Carter Holt Harvey	Hancock	64,000
2004	New Zealand (Tarawera Forest)	Fletcher Challenge*	Hancock	36,200
2006	New Zealand (Kaingaroa Forest, etc.)	Fletcher Challenge*	Harvard	166,000
2006	New Zealand (misc. regions)	Fletcher Challenge*	Pru Timber	65,000

*Either Fletcher Challenge Forests (a publicly listed company) or partly owned subsidiary endowment contributions without the added costs of borrowing fees from banks. Less favourably for forest grower countries, the TIMOs' commitment could end very quickly with onselling (Neilson and Evans 2009). That can occur when the forest asset values have appreciated to the point when onselling becomes too attractive to resist, or it becomes necessary to cover needed payouts, or it might be premeditated from the outset. Whatever happens, the situation militates against long-term commitments to R&D activities. Moreover, the TIMOs' forestry operations, especially within individual countries, typically belonged within very broad risk-spread portfolios.

A strong driver of forest ownership changes in New Zealand was the effective collapse of the Fletcher Challenge corporate empire around 2000. As a result Fletcher Challenge Forests (FCF) went from owning or managing 275,000 of forest (almost all radiata) in the key Central North Island Region around the end 2002 to none by early 2004. Prominent among the several causes of the collapse was the disastrous acquisition of UK Paper (Wallace 2001), but there were other factors. In acquiring state-owned forests in the region in 1996 FCF hoped to secure a strong revenue stream, but a financial crisis in East Asia soon reduced that sharply. In trying to maintain net cash flow, FCF over-cut their forests, harvesting stands while they were still too young, and further compromised future value by cost-cutting measures. This was part of a pattern in New Zealand at the time—failing to achieve makeable returns on radiata plantations by pursuing what proved to be unmakeably high rates of return.

In New Zealand, there were two notable exceptions, both in Asian ownership, to the trend against vertical integration. Ernslaw One, which is Malaysian-owned, holds around 70,000 of radiata plantation. Juken Nissho New Zealand, a Japanese-owned company holding around 50,000 ha of radiata, was the other, although it has recently done partial de-integration. Juken Nissho was also notable for not following the widespread trend towards shortening rotations for radiata.

In South Australia, privatisation has involved a major sawmill at Nangwarry which was specifically designed to cut radiata timbers. The New South Wales state forests, which contain the largest resource of radiata plantations in Australia, are now vested in Forests NSW, which is a state trading enterprise within the NSW Department of Primary Industry. The nature of Forests NSW as a trading enterprise is drawing speculation concerning its possible future privatisation.

In New Zealand there is also the complication of much forest land being vested in Maori ownership, with forest ownership taking the form of finite-period management and cutting rights. The split between land- and forest ownership does not of itself favour commitment on the part of forest owners to supporting long-term R&D.

In New Zealand the privatisation of state-owned forest plantations was essentially complete by 1996. Forest ownership, however, was not thereby stabilised. Indeed, the passing of Kaingaroa Forest and nearby areas of other former state-owned forest plantation into the hands of Harvard, to become the entity Kaingaroa Timberlands Ltd, took place in several steps. Along the way, the controlling owners made part-sales of the forest assets in order to dilute their business exposure to the forest holding. Moreover, these forest assets have since changed hands again, into a consortium of a New Zealand pension fund, a Canadian one, and a local Maori tribal incorporation.

Following the dissolution of the Forest Service in 1987, its suite of plantations was subject to land claims in connection with New Zealand's founding Waitangi Treaty of 1840, which are still being settled. This often leaves the forest owner effectively operating on a forest management licence with the land title vested in Maori interests. Encouragingly, however, Maori ownership of New Zealand plantation forests, in addition to just the land under them, has increased in recent years, and may well increase further. This promises greater future commitment to supporting radiata R&D, and some has started to materialise.

In New Zealand the economic context has changed markedly in the last few years. The dairying sector has experienced a strong boom. At the same time, the Global Financial Crisis, which began in the US in 2008, has severely affected the forestry sector. The resulting acute recession in the US housing industry, and associated weakening in the US dollar against the New Zealand dollar, severely depressed that key market for high-quality appearance-grade timber at a time when very large volumes of pruned logs were coming on stream. Even for other export markets, a strong New Zealand dollar, driven by the dairying boom, much reduced the profitability for forestry and forest products. Between these factors, and fears of carbon-market penalties arising from government management of that market, around 58,000 ha of plantation forest land was converted to dairying between 2008 and 2013 (Fallow 2013), despite major concerns about its effects on water quality in streams and lakes. These developments were surely having adverse flow-on effects for R&D expenditure in the forestry and wood processing. The adverse effects on wood exports, however, became mitigated by increased demand for wood in China, albeit primarily for lower-quality logs. Also reassuring is a very recent upsurge in the US housing market. Moreover, since mid-1994 international dairy prices to the farmers have fallen by over 50%. Furthermore, recent economic analyses (Monge et al. 2016; cf Yao et al. 2017) have explored the significance of likely dollar values of environmental externalities associated with intensive dairy farming compared with plantation forestry, showing forestry to be a much more economically competitive land use than was widely assumed. In fact, one major operation converting land from forestry to dairying has been terminated, albeit shortly before its completion.

A recent overview of the role of forestry—and by implication radiata—in New Zealand's economy is given by NZIER (2017).

In **Chile**, the forestry sector has tended to consolidate, with the two main corporate groups, Arauco and Mininco which are both controlled by Chilean families, becoming increasingly dominant. This has been especially in respect of new planting and industrial ventures, although a number of significant parcels of radiata plantations have changed hands, with the effect of medium-sized forest owner companies tending to disappear. Pulping capacity has continued to increase, by around 800,000 tonnes to nearly 3 million tonnes of radiata pulp (almost all chemical) per year, plus over 2 million tonnes of eucalypt pulp (J.C. Carmona pers. comm. 2012). Vertical integration remains a feature of the forestry sector there, unlike in other grower countries.

An important development in the context for forestry in Chile has been increasing acceptance of wood as a building material. This was long overdue in the light of how well wooden buildings withstand the earthquakes that occur there.

In **South Africa**, ownership changes of forests continued (John Mather pers. comm. 2011). The commercialisation of state forest plantations into the state-owned company SAFCOL was completed by 2000. This process, however, entailed the transfer of a high proportion of the radiata plantation estate to state conservation areas, which also entailed effective loss of a high proportion of the experimental trials. The remainder of the state-owned radiata plantations was privatised to Mountain to Ocean Forestry Company (MTO), which was then effectively cut off from all expert advice and assistance from SAFCOL. In turn, MTO was sold to Cape Pine Investment Holdings, which has since been sold to Global Environment Fund in which it remains a separate business arm. Website figures (http://www.capepine.co.za 2012) indicate that current holdings of radiata plantation are about 24,000 ha. Most radiata plantings in South Africa, however, have become subject to heavy post-planting losses from pitch canker infection that had originated in the nurseries (Sects 7.3.1, 7.3.2, 7.3.5).

The widespread abandonment of vertical integration of forestry, wood processing and marketing generally continued, except in Chile. In addition to the sale of the state-owned sawmill in South Australia, the two state-owned sawmills in New Zealand were sold separately from forest holdings.

7.2.2 R&D Organisations

For various reasons, the major publicly funded R&D organisations serving the forestry sectors tended to come under increasing pressure. Governments were under a two-way squeeze, coming under political pressure to reduce tax levels and expenditure, and yet facing increasing welfare budgets that were largely driven by a combination of ageing populations and ever-increasing costs of advancing medical technology.

Government support for R&D tended to become contingent on support from industry. Meanwhile, foreign ownership of commercial forests was increasing greatly in New Zealand and Australia. Foreign owners of both forests and industrial plant have typically represented large, multinational interests. As such, they typically had their own technology units which they might turn to, particularly for wood processing. Also, some of the risks associated with huge local dependence on radiata were often easier for such owners to address by global risk spread than by supporting R&D to develop active but expensive countermeasures to those risks. Smaller forest growers, while collectively a large element in New Zealand, were typically not funders of research. Despite being a very diverse group, they shared another feature, in their forestry interests very often being parts of risk-spread portfolios. Thus there were forces militating against industry support of government research organisations, and thence against sustained government funding of them.

We trace here the fortunes of several key R&D institutions, but do not try to cover all the advisory committees that were created and made input. With increasing privatisation of radiata-associated R&D institutions, as well as of radiata plantation, interrelationships have become more complicated. New institutions have resulted in both new alliances and new competitive relationships, with scope for conflicts. Notably among the changes, the traditional territoriality that existed among the state forest services within Australia has been much reduced.

In Australia, CRCs (Cooperative Research Centres) were created, linking government research organisations, universities and industry organisations. Some forestry research involving radiata proceeded under the CRC for Sustainable Production Forestry, based in Hobart and involving four universities, which was established in 1997 and gave way to the CRC for Forestry in June 2005 which itself was terminated in June 2012.

A more specialised organisation, PLANTPLAN, continues some research in conjunction with servicing the Southern Tree Breeding Association and other plant breeding programmes.

In 2001, the Forest and Wood Products Research and Development Corporation (FWPRDC) was set up in Australia to gather and disburse research funding. It was converted in 2007 into FWPA (Forests and Wood Products Australia), a non-profit industry-owned organisation with a strong focus on radiata. Among its activities was the Juvenile Wood Initiative (JWI) to research corewood properties of radiata, largely with a view to improving them through genetic selection. FWPA soon became included in New Zealand's Wood Quality Initiative, as an "additional stakeholder." Among other things, the JWI corewood research entailed considerable emphasis on attaching economic weights to genetic improvement of various wood properties relative to each other and to gains in volume of wood produced, in collaboration with both STBA and CSIRO. This endeavour was much simplified by the pre-eminence of light structural timber in Australia's end-product mix for radiata. However, a major imperfection in the log market in Australia has been exposed by finding very different sets of economic weights among traits for forest growers and sawmillers respectively (Ivković et al. 2006).

Despite such R&D activities and support for them, the general level of industry's political support for CSIRO [Division of] Forestry and Forest Products (FFP) dwindled to the point that the Australian government decided in 2008 to disband it. From that institution, which had a convoluted history (CSIROpedia 2013), a few researchers involved in radiata were then assigned elsewhere in CSIRO, relying on STBA and FWPA for funding support. Some CSIRO scientists had by then embarked on genomic research with radiata, with a major emphasis on discovery of genes controlling wood properties (e.g. Dillon et al. 2010), and such research is continuing within CSIRO's Division of Plant Industry.

The disbanding of CSIRO FFP was seen by Kile et al. (2014) as largely a "downstream" consequence of privatisation of plantation forests combined with abandonment of vertical integration, but Ferguson (2015) saw it more in terms of a loss of "strong linkages and networking between research organisations and research users."

An operational merger between CSIRO FFP and the New Zealand Forest Research Institute Ltd (branded as Scion from 2005) was attempted in 2004, in the form of an Unincorporated Joint Venture, Ensis. This, however, did not deliver the hoped-for benefits and proved essentially unworkable. Among other things, the links of Ensis with both STBA and RPBC, which were competing organisations, were causing much unease. The merger was formally reversed on 31 December 2007.

In Australia, the STBA developed a comprehensive data management system that was running in 2000. From that, through the Animal Breeding and Genetics Unit (AGBU) of University of New England, Armidale, NSW, scientists developed TREEPLAN®, a software package to make full use of all available pedigree information to evaluate breeding values of selection candidates. Operational use of TREEPLAN began with radiata, in 2002 (Wu et al. 2007a), and has since been extended to other tree species, in Australia and overseas. In addition, the STBA became heavily involved in the breeding of shining gum, *Eucalyptus nitens*, which had come to be planted on a large scale for pulpwood. In 2000 Western Australia's government agency exited from STBA, and soon afterwards Queensland's withdrew from breeding radiata in favour of buying its seed on the open market.

Within **New Zealand** the RPBC (Radiata Pine Breeding Cooperative) became a limited liability company (LLC) in 2001, renaming itself Radiata Pine Breeding Company, but with little immediate change in how it operated apart from greater autonomy in its financial management, and no change in the RPBC brand. Nominally at least, RPBC and Scion were designated as a consortium in 2005 for negotiating government research funding which matches industry contributions. Funding from industry, however, for some years tended to remain effectively static, despite the inducement of matching contributions from government sources. Moreover, radiata breeding research is funded on the basis of individual projects, for which contracts are awarded to a variety of providers. Actually, RPBC, like STBA in Australia, has come to represent a separation between operational breeding and associated R&D instead of tree breeding being done within R&D organisations.

In 2013, the RPBC, after Antoine Kremer of France joined Andrew Granger and Christine Dean on its advisory board, embraced research on **genomic selection**$^{\mathbf{G}}$ (Sect. 7.11.1.4), with emphasis on selecting for both disease-resistance and wood-properties. This move was accompanied by much-increased financial contributions from PRBC and increased co-funding from government.

In 2003, another government-sanctioned consortium between industry and the government's research funding agency and industry came into being, with FRI heavily involved in the actual research. Originally called WQI (Wood Quality Initiative), it was superseded in 2009 by SWI (Solid Wood Innovation). WQI and then SWI addressed a broad range of research on radiata's wood quality, including prospects for genetic improvement. SWI has maintained its link with Australia through FWPA upon expiry of its Juvenile Wood Initiative (JWI) programme.

In 2007 another such consortium, Future Forests Research (FFR) was set up, involving Scion, industry and Government. It includes almost all areas of commercial forestry research for New Zealand that were not covered by existing consortia. With NZRPBC thereby excluded, FFR has operated with a major emphasis on intensive silviculture of radiata. In 2017, FFR was renamed Forest Growers Research Ltd (FGR), with some changes to its mandate.

Changes also occurred in the Centre for Advanced Biotechnology Te Teko which was started by Tasman Forestry Ltd and had gone through several ownership and name changes; for a while the Centre was under the brand of Fletcher Challenge, and then Horizon 2 after the Fletcher Challenge corporate empire disintegrated. In the Tasman and Fletcher Challenge days, during 1994–1999, co-author WJL was engaged there for part of each year 1992−1995. In 2007 the Centre was taken over by the biotechnology company ArborGen Inc., which itself was the outcome of similar institutional and name changes in south-eastern USA and took over remaining assets from CellFor (another biotechnology company) in 2012.

A separate company, Forest Genetics (FG), was started in 2002 by Mike and Sue Carson, both formerly of NZFRI, to develop and market for commercial forestry their own radiata clones, descended from the New Zealand radiata breeding programme. They were joined by Christine Te Riini, formerly in charge of genetic improvement of radiata at Te Teko with 10 years' experience with clonal research and deployment there. FG's operation grew to include a major programme of testing a set of clones on multiple sites in New Zealand and Australia, and contracting out the propagation of their selected clones to commercial nurseries. FG was a member company within the RPBC. Since its inception, FG has taken on Kaingaroa Timberlands as a shareholding partner.

Alliances involving tree-breeding and research agencies and biotechnology companies have formed and evolved. During this period there were some takeovers or mergers involving the biotechnology companies, with changes in some of the competitive interrelationships.

In **Chile**, the breeding Cooperativa has remained in place, with more integrated management of breeding material among member companies, in contrast to the earlier model of persisting with essentially individual breeding programmes. Thus the role of the Cooperativa has continued to centre on setting and communicating protocols for operational breeding practices, reporting on activities and carrying out some data analysis. Two changes occurred around the start of the chapter period. First, Roberto Ipinza left his post of Director in 1997, with Heidi Dungey taking over as acting Director under the tutelage of the founding Director, Roberto Delmastro. Then, in 1998, Fernando Droppelmann returned as Director and still holds the post.

However, in 1997 a major change in Cooperativa membership came; one of the two main corporates, Mininco, opted out of the Cooperativa, to run its own breeding programme, with Tim White of University of Florida as external consultant. The Mininco group currently holds around 335,000 ha of radiata in Chile. Among the remaining membership, the Arauco group with ca 615,000 ha of radiata (Arauco 2012) is, through its subsidiary Bioforest which is led by Claudio Balocchi, now greatly pre-eminent within the cooperative. Bioforest is a large organisation in itself, with some 130 employees, and is involved in a wide range of forest research including eucalypts as well radiata.

A high proportion of Chile's research relating to radiata has continued to be done within various universities, commissioned with varying levels of contestability by a mix of individual companies, industry advisory bodies, and several government agencies with research funds to disburse. Among the participating universities, the University of Concepción has been playing an increasingly prominent role, as befits the proximity of Concepción to much of Chile's forest plantations and wood-processing plants. Among the governmental commissioning agencies has been CORFO (Corporación de Fomento de la Producción). Importantly, CORFO has facilitated setting up the Biotechnology Centre in the University of Concepción. This centre has a broad portfolio of projects involving radiata, ranging from pulping technology to genomic studies as a prospective tool for selective breeding. Major companies with their own research facilities are the Arauco group, in its subsidiary Bioforest SA, and the Mininco group. Bioforest has focused heavily on clonal propagation with large numbers of clones cryopreserved, and is pursuing other biotechnology including genomic selection. Within Mininco a radiata breeding programme now operates separately from the Cooperativa. Another national agency, Fundación Chile, was involved in developing technology companies to promote clonal forestry, but with only two major prospective clients could not strike a deal. In fact, the forestry department of Fundación Chile has now been abolished.

As elsewhere, intellectual property associated with breeding radiata in Chile has often been sequestered within by individual corporates rather than shared, despite the presence of the Cooperativa.

In **Spain** active research on quantitative genetics and breeding of radiata is proceeding in Pontevedra in Galicia, while the research effort on radiata breeding in the Basque Autonomous Region has been dropped in favour of a focus on propagational and genomic biotechnology.

7.2.3 Non-governmental Organisations (NGOs)

Among NGOs, historical objections to plantation forestry have increasingly given way to at least some acceptance. This acceptance is for both the potential to relieve exploitation pressures on natural forests and an appreciation of the more direct environmental services that plantations can provide, such as checking soil erosion, preserving water quality and sustaining populations of birds and even bats.

For growing radiata, amongst forest plantations in general, the Forest Stewardship Council (FSC) has become increasingly influential. It promotes and operates the certification of forest products as having been sustainably produced, placing pressure on retail outlets, especially in North America and Europe, to sell only compliant products. It has also generated business for certifying agents who scrutinise the processes of growing and harvesting.

The basic objectives of third-party certification are entirely worthy, but some proscriptions of acceptable growing practices are a concern, involving some fundamentalist positions and a poor appreciation of some local biological realities. For example, there is an absolute refusal by some such NGOs to contemplate participant growers being involved in field research on genetic engineering (GE), let alone adopting it operationally. Indeed, certain positions taken by certifying NGOs could even be counterproductive, given that they can both impede or discourage plantation forestry in general and block use of some biotechnologies that may be environmentally beneficial.

7.3 Forestry Activity and Problems

7.3.1 New Planting and Retirements

From 1998 onwards new plantings of radiata have been relatively limited, for a variety of reasons, including economic and biotic factors. Indeed, some significant areas of radiata plantation have been converted to other land uses, including cases of very young crops. Nevertheless, there is a portent, from the 2015 UNFCCC conference, that this trend could be reversed.

In **Australia**, new planting of radiata has been largely replaced by a boom in planting eucalypts, mostly Tasmanian blue gum (*Eucalyptus globulus*) (Ferguson 2014). With the promise of high returns from short, pulpwood rotations, and some tax advantages, various private forestry ("prospectus") companies, termed Management Investment Schemes, have been formed to plant eucalypts. Many of these eucalypt plantings, however, have under-performed, largely through planting on inappropriate sites, while key tax advantages had been withdrawn in South Australia in 2000, so this boom is over. Meanwhile, companies owning radiata plantations have tended to consolidate their holdings, often following or pending ownership changes (Table 7.2).

In **New Zealand**, the rate of new radiata plantings (MPI 2013) fell steeply (Figure 3.1) after 1996 following a recession in south-east Asia, and almost ceased around 2006 although harvested areas were mostly restocked. Since then, however, there was been a slight upturn with around 12,000 ha of new planting in 2011, compared with around 6,000 ha in 2010, although not all would be with

Table 7.2 Areas of different conifer species ('000 ha), by States, in Australia as at 2012 (ABARES)

State	Radiata pine	Maritime pine	Southern pine	Hoop pine, etc.	Total
New South Wales	277	0	12	7	296
Victoria	226	0	0	0	226
South Australia	129	0	0	0	129
Tasmania	75	0	0	0	75
Western Australia	56	42	0	0	98
Capital Territory	8	0	0	0	8
Queensland (&NT)	1	0	139	50	189
Total	772	42	151	49	1,024
Percentages	75.4	4.1	14.7	5.7	100

radiata. In recent years there has tended to be consolidation of forestry operations, following ownership changes. From 2003 (NEFD 2013) to 2012 New Zealand's total forest plantation area actually declined by around 5% (*op. cit.*), due mainly to a dairy farming boom, and the conversion of plantation land to dairy farms would have been almost all from radiata. Harvesting and restocking with radiata had been running at around 40,000 ha per annum (NEFD 2013, Figure 2.1), while average recovered yields per hectare rose from around 460 to around 525 m^3 per ha. In younger radiata plantations pruned area declined from 67 to 58% and areas commercially thinned declined from 21 to 17% (Table 7.3).

At one stage in very recent years, a strong market for carbon sequestration credits was starting to boost new plantings. Then, however, a collapse in carbon-credit prices was allowed to spread from eastern Europe where carbon credits had been granted to encourage compliance that did not eventuate; that created an incentive to liquidate forest plantations and many in New Zealand acted accordingly. Fluctuating planting rates are a worry for the future of the forestry sector, in which capital-intensive processing plant will depend heavily on continuity of supply of raw material.

Investment in major processing plant has lagged in New Zealand, with even some retrenchment in pulping and papermaking. By contrast, exports of unprocessed logs have boomed, making New Zealand the biggest such exporter globally. That is preventing the local supply of the sawmilling residues needed to justify building new and profitable pulping plant (Hall 2016).

In **Chile**, new planting of radiata has slackened significantly, averaging less than 20,000 ha per year from 1998. This probably reflected several factors: considerable planting of eucalypts mainly for short-fibred pulpwood; some concerns over European pine shoot moth deforming stems; and concerns over arson blamed ondisgruntled native Americans. The forestry encouragement scheme, under D.L.

Table 7.3 Geographic distribution of radiata plantation ('000 ha) in New Zealand as at April 2012 (NEFS)

Island	Wood supply region (Fig. 7.1)	Latitude range (°S)*	Seaboard(s)	Area
North	Northland	34½–37	W–E	197
	Central North Island	37–39	W–NE	519
	East Coast	38–39	E	149
	Hawke's Bay	39–39½	E	127
	Southern North Island	39–41½	W–E	160
	Total North Island	34½–41½	–	1,152
South	Nelson/Marlborough	41–42	N–NE	155
	West Coast	42–43	W	23
	Canterbury	42½–44½	E	83
	Otago/Southland	45–46½	S–E	130
	Total South Island	41–46½	–	391
National total		34½–46½	–	1,543

*Approximate range of concentrations

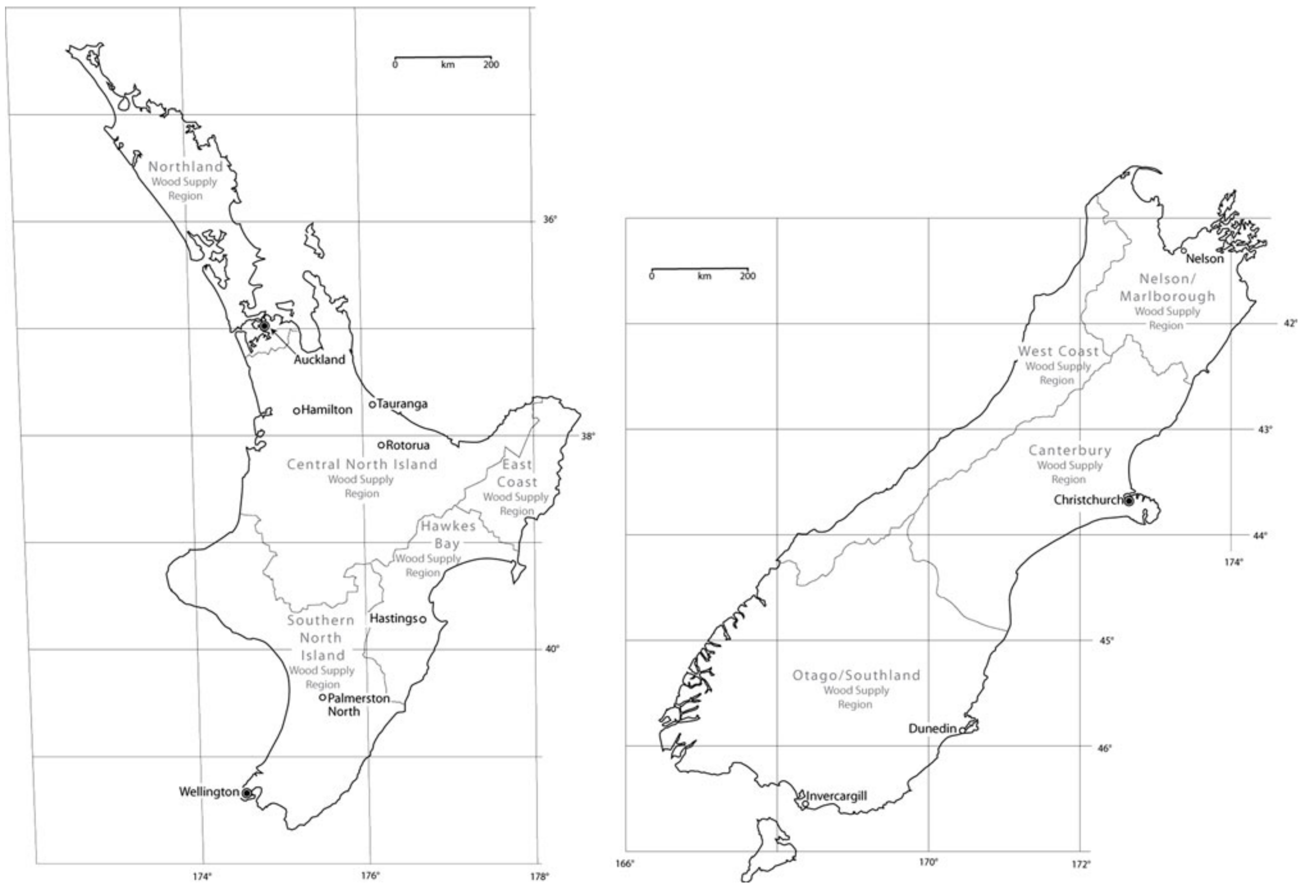

Fig. 7.1 Maps showing wood supply regions in New Zealand, right, South Island, left, North Island (After NEFD 2016, permission Ministry of Primary Industries)

701, which had effectively run on for many years after its original expiry date, was renewed as at 1 January 2013, but with focus on both encouraging small landowners and rehabilitation of degraded soils (Anon 2013).

In **Spain**, however, new planting of radiata accelerated, especially in the province of Galicia, largely through European Community encouragement of afforestation of marginal agricultural land (Zas and Serrada 2003). By 2001, the recorded radiata plantation area had increased to 291,000 ha (R. Zas pers. comm. 2012). However, the annual planting figures have been volatile, reflecting some biotic alarms over radiata, some surges in prices for hardwood pulp logs and a regional slump in softwood log prices caused by massive salvage logging of maritime pine following an extreme storm in south-west France in 2009.

In **South Africa** new plantings of radiata virtually halted, what with changes in forest ownership (Sect. 7.2.1) and increasing concerns over pitch canker (Morris 2010, Mitchell et al. 2011). Indeed, the area of commercial radiata plantations has shrunk, with retirement of some land to conservation estate and not replanting with the species on account of problems with pitch canker. It was reported (DAFF 2010) that, as at 2008/2009, of a total listed area of 58,000 ha previously occupied by radiata, nearly 18,000 ha were “temporarily unplanted,” and the area of 1- and 2-year-old radiata plantations had fallen to under 500 ha compared with around 1000 ha in each of the remaining annual age classes up to around 10 years.

7.3.2 Developments in Forest-Growing Practices

In **Australia**, the developments have been modest. Because of several factors, including the pre-eminence of the market for light structural timbers, and the sometimes profitability of commercial thinning, changes to silvicultural regimes for radiata have been less radical than in New Zealand. That meant less readjustment when problems with radical regimes came to light. Even so, stockings tended to be reduced and rotations shortened in comparison with the past.

In New Zealand especially, TIMOs were making changes in silvicultural regimes. They were effectively working to lower discount rates which reflected lower costs of investment money, and which in turn made more attractive the economics of longer rotations. One overseas-based company, however, had embarked on a dramatic but ill-fated experiment on cost-cutting, planting radiata at near-final stockings and doing almost zero tending (Dyck and Thomson 1999; Sutton 1999); subsequently, the resulting stands got largely converted by a new owner to dairy farming. Anyway, rotation ages have typically extended from 24 to 27 years to 30 to 34 years, although this has brought concerns over more heartwood which is unwanted because its appearance is disliked by many end-users and it is neither reliably durable nor reliably treatable with preservative. Also, final-crop stockings have tended to rise from around 200 to around 300 stems per ha. For the decline in the percentage of stands being pruned there are several reasons. In some cases there were the cost savings driven by immediate financial liquidity problems. Labour availability was often a problem. Moreover, a decline in the USA market for high-quality clear timber, and a boom in the Chinese market for logs (Katz 2013) with limited price premiums for quality, have doubtless influenced perceptions of the profitability of pruning which is done at some sacrifice of wood volume. Yet, if countries like China and India eventually become premium markets for radiata clearwood, failure to prune might prove costly, especially with the widespread problem of achieving high wood stiffness with radiata in New Zealand.

While New Zealand has long used almost exclusively bare-root planting stock for establishing radiata, several major nurseries have begun large-scale production of container stock. That extends the planting season, can reduce post-planting toppling and subsequent butt sweep, and promises more efficient use of scarce seedlots and cuttings material of top genetic quality. Using container stock may also compensate for some loss of field-planting skills arising from continuing rapid changes of personnel.

Reported percentages of cuttings in total nursery outturns of radiata (J. Novis, pers. comm. 2013) have fluctuated somewhat erratically (Table 6.8). Figures are by no means complete, but there was an increase from 30% in 1997 to 43% in 1999, falling back to 30% in 2003. Figures are available again from 2006–2010, varying from 34% in 2006, 23% in 2007 and 27% in 2010.

In **Chile**, no radical silvicultural changes occurred for radiata, there remaining a broad mix of regimes according to markets, terrain and site quality. By 1997, however, a substantial shift to using cuttings rather than seedlings had already been made in order achieve faster capture of the latest genetic gains from breeding (Balocchi 1997), and Arauco has been using nearly 100% cuttings for radiata planting from 2001 (Balocchi pers. comm. 2014). Arauco also made a massive shift to using container rather than bare-rooted stock; while more labour-intensive, it has served to give more efficient capture of genetic gain, and is evidently preferred for the relatively sticky soils on which much of the plantation estate grows. The other main corporate, Mininco, has not made the same wholesale conversion to container stock, having large areas of sandy or scoriaceous soils. On these poorer soils, radiata is often grown as dedicated pulpwood crops and post-planting toppling of trees is not the same issue.

In **South Africa**, the challenge has been to accommodate early mortality of radiata associated with pitch canker infection acquired in nurseries, with the complication that pitch canker has recently been found affecting older trees (Mitchell et al. 2011). Accordingly, screening for genetic resistance to canker is being intensively practised, and vigorous efforts are being made to hybridise radiata with more resistant species (A. van der Hoef, pers. comm. 2014). The eventual success is not yet known, but it will probably determine the future usefulness of radiata in South Africa.

In **Spain**, pulpwood and roundwood regimes for radiata have been mostly abandoned in favour of producing sawlogs (Rodriguez et al. 2002), with or without commercial thinning. Regimes envisaged range from 325 to around 500 stems per hectare at harvest, with rotations from 25 to 35 years, depending on site quality and ownership. Most of the Basque Country plantations that are communal forest have been managed by the regional Forest Service. For the Galicia Region much seed, from seed orchards, has been imported from New Zealand.

7.3.3 New Decision-Aid Software and Remote-Sensing Technology

Underpinning leading-edge plantation-forestry practices have been major advances in the continuing development of prediction tools for wood yields and log- and wood properties, which serve as decision aids, and are becoming increasingly linked to the availability of new remote-sensing technology. Radiata, because of its plantation-forestry status, has been heavily involved in these developments.

In New Zealand, a key resource for the growth modelling is the national Permanent Sample Plot (PSP) database, which as at 2007 comprised records of regular assessments of ca 27,000 PSPs (Hayes and Andersen 2007). These plot data have come largely from PSPs in radiata stands, nearly half of them being still current. Continuing software development work for modelling radiata crop development has been undertaken by both ATLAS Technology, a subsidiary of Scion (New Zealand Forest Research Institute Ltd), and independent operators. Harnessing databases and models concerning variation in wood properties according to site, silviculture, genetic status and tree age (e.g. Watt et al. 2011, 2013), prediction tools and decision aids for forest managers that involve all stages of the value chain have come available for radiata. The software, however, is mostly proprietary, needing to be purchased by users. Details are not only beyond the scope of this book but are also subject to continuing updating and refinement.

Aerial photography has long been available as a remote-sensing technology for forest management, but some of its role can now be supplanted by satellite imagery which has become much cheaper to access in recent years (Watt and Watt 2011). However, a major recent development in remote-sensing technology, is LiDAR (Light Detection And Ranging), which typically uses near-infrared light, in the manner of using radio waves for radar (Adams et al. 2013). It can be used to study numerous stand variables, and progress is being made in using it for inferring wood properties (Watt et al. 2013). With the availability of small drones (Unmanned Aerial Vehicles) remarkably detailed information on stand structure can be obtained and analysed.

These developments in use of remote-sensing technology and modelling of stand- and processing outturns serve to both reduce the physical tasks of obtaining information and allow managers to make better-informed decisions. Indeed, they make it possible to address questions that could not be effectively addressed in the past. All these developments have depended heavily on the continuing increases in computing power, but they still have their limitations. The genetic populations of radiata will remain a continuously changing variable. Moreover, there remain basic biological information gaps, as in how the trade-off between wood density and stem volume operates at the whole-crop level at harvest age.

7.3.4 Harvesting and Log Segregation

At harvesting, logs are cut into certain lengths and are then segregated into categories for processing, all with the aim of optimising net product value. Traditionally, logs have been segregated into categories according to size, taper, knottiness and straightness. For cutting to optimum lengths, a decision-aid programme that addressed changes in diameter up the stem had been developed and updated. But other bases for optimal cutting to length and segregation are also needed, including automatic adjustments for changes in market specifications. Pruned logs are an obvious category for special processing.

Individual trees of radiata can vary importantly in wood stiffness, which is often the main limiting factor for obtaining structural timber grades from unpruned logs. To deal with this, acoustic tools have been developed to grade individual logs for wood stiffness. These tools, which include the proprietary HITMAN and SWAT, use sound pulses into the ends of the logs. The pulses are reflected back from the opposite ends, and measure the rate of sound travel which depends on wood stiffness, thereby allowing a useful measure of stiffness. Those logs with the stiffer wood are sent to the sawmill for cutting into appropriate dimensions for structural timber, while those with less stiff wood are dispatched for cutting to dimensions for non-structural uses or else for pulping. The economic benefits of such segregation are substantial (Tsehaye et al. 1997).

7.3.5 Biotic Alarms

Several alarming outbreaks of diseases or pests have affected radiata in recent years, largely differing among countries.

Pitch canker is a fungal disease of pines, which is caused by a *Fusarium* species. It leads to shoot dieback and, when cankers affect the main stem and girdle it, can kill trees. Stem cankers typically develop slowly but steadily, and are distinctive on account of profuse resin bleeding. Hodge and Dvorak (2000), in an inoculation study, found radiata to be among the most susceptible host species. Pitch canker first became evident in and around native stands of radiata in California in 1976. There its incidence became alarming and, while it has since largely subsided, it has discouraged planting radiata.

The disease appeared in South Africa in 1990 (Wingfield et al. 1998), where it has since become troublesome. The pathogen has spread widely among forest nurseries, to cause considerable post-planting mortality. The first outbreak in a plantation of radiata there was in 2005, and was subsequently confirmed as pitch canker (Coutinho et al. 2007). Pitch canker has tended to discourage replanting of radiata (see DAFF 2010), but is being addressed by routine screening of intensively select parents for resistance.

Pitch canker has also appeared in both Chile and Spain. In Chile, it has not been reported as having caused the same trouble in plantations as in South Africa, perhaps because of a shortage of insect vectors compared with in South Africa and what appears to be relatively low climatic hazard (Ganley et al. 2009). In Spain, however, it is causing concern in the Basque Autonomous Region, leading to very little new planting and even a drop in replanting.

There the climatic hazard rates as high (*op. cit.*), while there are insect vectors that reportedly proliferate in log yards of processing plants leading to concentrations of disease nearby.

New Zealand and Australian radiata breeders have attempted proactive screening of select progenies for resistance by planting in a disease-hazard area in California, under the IMPACT project (Devey et al. 1999a). Although genetic differences in susceptibility within radiata had been observed in an inoculation trial (Matheson et al. 2006), there has been too little pitch canker in the field trial to resolve genetic differences in susceptibility. While there has been some shoot dieback there, it has since proved attributable to another, less alarming pathogen, *Diplodia*.

The presence of pitch canker in all three natural stands in mainland California now creates a major biosecurity barrier to tapping those stands for further refreshing the genetic diversity of domesticated stocks.

The **Monterey pine aphid**, *Essigella californica*, was discovered in 1998 in both Australia and New Zealand, and spread rapidly in both countries (Wharton and Kriticos 2004; Watson et al. 2008). Capable of debilitating trees of radiata under drought stress, it has caused alarm in Australia. However, despite fluctuations in abundance, it has not had disastrous effects there, let alone in New Zealand. It is suspected that some natural biocontrol has occurred.

Nectria, the fungus *Nectria fuckeliana*, was identified in the 1990s as a pathogen causing bad stem cankers following pruning of radiata in the south of New Zealand (Crane et al. 2009; Hopkins et al. 2012), despite it having no prior record as a damaging forest pathogen. It has since been identified as causing similar damage in radiata plantations in southern Chile (Morales 2009). After causing initial alarm, it appears to be controlled by avoiding winter pruning. This solution contrasts with practice in the north of New Zealand where summer pruning is often avoided because of the risk of stem cankers following infection by *Diplodia* (M.A. Dick pers. comm. 2012).

In Chile, in the Arauco Peninsula, a combination of very severe needle cast and considerable shoot dieback, which often killed very young radiata trees, was first observed in 2004 over 70 ha, the immediate cause being the fungus-like oomycete *Phytophthora pinifolia* (Durán et al. 2010). By 2006 the affected area had expanded to an alarming 60,000 ha, but mysteriously reduced to under 500 ha by 2008. Durán et al. (2008) reported the identification of the pathogen.

Similarly, the threat posed to radiata stem form in Chile by the European pine shoot moth appears to have receded, in this case largely through natural parasitoid biocontrol (Ramos and Lanfranco 2010: Mead 2013, Box 4.1). However, sirex (*Sirex noctilio*) was eventually reported in Chile in 2001 (Beėche et al. 2012). Its status there as a threat was accentuated by the importance of pulpwood production leading to maintaining relatively high tree stockings, but the threat has been mitigated by the successful introduction of a nematode and two wasp parasitoids (*op. cit.*).

However, another insect pest, the European gypsy moth (*Lymantria dispar ddispar*), has unexpectedly proved capable of causing complete defoliation and severe mortality in a pure radiata plantation in north-western Spain (Castedo-Dorado et al. 2016).

In New Zealand, a novel form of needle cast, "**Red needle cast**" (RNC), was observed in 2006, and recognised in 2008 (Dick et al. 2014), in some northern areas where needle casts had not hitherto been prevalent. It has caused severe defoliation, mainly in relatively old trees, but was evidently different from PNB (physiological needle blight), a needle cast of radiata that had long occurred sporadically following wet winters in the north of the country but could not be related to any actual pathogen. RNC has since been associated mainly with a newly discovered oomycete, *Phytophthora pluvialis*. It has spread over a wide geographic area within the North Island, being associated with mists on ridges or general humidity on lower ground. Its final extent and significance are still unclear, but it is spurring considerable research.

Thus, since around 1997, three diseases appeared in radiata, which exhibited alarming symptoms and threatened to spread widely. While the initial threats have generally not materialised into serious and widespread losses, a worrying common feature is that they have all been caused by fungi or oomycetes with no prior record of being significant pathogens. Meanwhile, some foliage diseases that had become "traditional" in radiata, notably cyclaneusma needle cast and dothistroma needle blight, remained as greater or lesser nuisances, according to local climates. In response, there has been a very recent move within New Zealand to escalate research on the development of genetic resistance in radiata to both the new and traditional diseases. One avenue of research is the search for cross-resistance whereby the same individuals can be selected effectively for resistance to more than one pathogen (S. Kennedy et al. in prep.). For these endeavours, a broad range of technologies is being enlisted.

7.3.6 Weeds and Related Issues

In addition to pests and diseases, weeds have tended to become an increasing problem over time, involving plantation forests in general and not just radiata. Typically, weeds are easily dispersed and far more easily established than eliminated, leading to progressively increasing suites of weed species that depress tree growth by competition and/or inflate plantation-growing costs. Use of fire to remove logging residues and help control weed growth has been widely discontinued, on various environmental grounds. While some traditional herbicides are becoming outlawed, new and more benign and selective herbicides have been developed.

An example of a weed acquiring relatively recent prominence in forest plantations is *Buddleia davidii* (Fig. 7.2) in New Zealand, which has spread very rapidly. Indeed, *Buddleia* has become so troublesome as to be targeted for biological control; for that, a parasitoid *Cleopus japonicus*, the buddleia leaf weevil, has been successfully introduced and promises significant control (Watson and Withers 2012) (Fig. 7.3).

Fig. 7.2 Buddleia plant in flower, Rotorua, New Zealand. The species is an imported ornamental shrub that has become invasive in forest plantations

Fig. 7.3 Buddleia plants showing damage from the *Cleopus* weevil

7.3.7 The Advent of "Carbon Forestry"?

Concern over the build-up of atmospheric carbon dioxide (CO_2) and consequent global warming has created a market for growing crops that sequester large quantities of CO_2 (Manley and Maclaren 2009). This has stemmed from the Kyoto Protocol of 1997 in which various countries committed themselves to certain net reductions in CO_2 emissions. Despite obvious deficiencies in the agreement, stumbling progress, and much current uncertainty, a market developed for "carbon credits". Radiata, having quite wide site tolerances and being generally grown on the comparatively long rotations needed for producing solid-wood products, is very suitable for carbon sequestration, with the bonus that such products have service lifetimes that mean sequestration that continues long after crop harvest.

An established, reliably high-value market for carbon credits has potentially very important implications for growing radiata. It creates an obvious encouragement for new planting, raising the profitability of plantations. This is especially so where there is pastoral land of marginal or negative profitability, which is the present situation in New Zealand. But carbon credits also lengthen the economically optimum rotation (Manley and Maclaren 2009) and favour higher stockings (cf. Kimberley et al. 2005). In turn, the longer rotations and higher stockings will mitigate the problems with radiata's wood quality, making less urgent the need for genetic improvement in this respect.

However, the impacts of "carbon forestry," while potentially great if certain shortcomings of the Kyoto Protocol are rectified, have recently become problematic. Since the global financial crisis that began in 2008, eastern European countries have been selling 'carbon liabilities' at progressively decreasing prices. In New Zealand, where the management of liability regulations has led to some perverse features and the government has not imposed a minimum carbon liability price, the cheapness of such liabilities has created a scramble to liquidate large areas of forest. This resulted in a reversal from a brief carbon-driven upsurge in planting, and conflicts with some pressing needs for soil conservation and catchment protection.

7.4 Operational Breeding and Deployment Activities

The five main grower countries all had up-and-running breeding programmes, which were set for continued advancement, maintaining cycles of evaluation, selection, intermating, testing, evaluation, and so on. However, the emphasis in breeding goals has changed appreciably in New Zealand and Australia, with an increased focus on improving several wood properties, in some trade-off with the emphasis on past breeding objectives. Indeed, this shift has driven much of the research and breeding activity since the mid-1990s. With the shift, and problems with maintaining and evaluating some progeny trials resulting from institutional turbulences, emphasis on fast turnover of generations in New Zealand and Australia has reduced, despite active research on improving early selection on young progeny.

Also, since 1997 there have been revisions of the underlying breeding strategies for radiata in both New Zealand and Australia (Sect. 7.8.2).

7.4.1 Australia

Australia's largest forest owner, State Forests NSW, has remained within the New Zealand RPBC. As a full member, it has exercised substantial influence in shaping RPBC's research programme, especially in the area of genotype-site interactions which are more important in many parts of Australia than in New Zealand.

The STBA has continued to service radiata breeding in the rest of south-eastern Australia, along with breeding of temperate eucalypts, principally shining gum, *E. nitens*.

7.4.2 New Zealand

In New Zealand, radiata breeding was affected by indifferent success of progeny trial plantings from the 1985−1988 round of fresh plus-tree selection, which resulted largely from disruptive management changes in some forest-owner companies. A further blow came when a promising progeny trial was virtually lost through defoliation by caterpillars of *Helicoverpa*, the tomato fruitworm. This was an unforseen consequence of establishing *Lotus preunculata*, which was intended to provide fodder for grazing cattle in the forest, but was attacked by the moth whose caterpillars turned to the pine foliage after running out of the *Lotus*. These problems have slowed the turnover of generations.

Breeding operations, namely assessments, selection, intercrossing and establishment of progeny trials have continued, albeit under revised selection criteria (Sect. 7.7) and an evolving strategy (Sect. 7.8.2.2).

Meanwhile, establishment of new genetic gain trials, especially ones containing the large plots needed give a measure of whole-crop performance, had been restricted by budget levels for breeding. Given the need for continued economic justification of further genetic improvement, and increasingly evident problems of assigning relative weights to growth rate, tree form and wood properties, this restriction has led to some troublesome information gaps. Since adverse genetic correlations among traits are involved here, weighing up the economic worth of the various traits is extremely important, but it is actually very difficult.

In deployment of genetically improved planting stock there were fluctuations (Table 6.8). Two contributing factors were fluctuations in both planting programmes and seed supplies, the latter being influenced by some seed orchards being phased out and others coming into production. The percentage of deployed planting stock that rated GF19 or higher rose from 11% in 1997 to 16% in 2003, ranging from 39% to 47% during 2006–2009, but dropping to 28–31% in 2010–2012. In 2008, there was a shortfall in open-pollinated seed orchard seed, leading to "Stand select" seed collections made within stands of seed-orchard source: such seedlots are of unproven genetic merit and uncertain breadth of genetic base, and therefore entail some elevated genetic risk. Apart from this brief episode, the pattern has been a progression towards greater use of vegetative multiplication in order to accelerate capture of genetic gain, followed by increasing large-scale deployment of specific and progressively better characterised clones.

7.4.3 Chile

Since 1997, there have effectively been two radiata breeding programmes running, under the Arauco and Mininco groups. Within each of these programmes, however, there has been amalgamation of breeding programmes, instead of the original disconnection among the programmes of the original individual member companies. Turnover of generations has been accelerated, pressing on to producing some third-generation breeding-population material by the early 2000s. This has been helped by switching to simpler mating designs within breeding populations. As elsewhere, there has been an increasing focus on wood properties. The arrival of the pine shoot moth in Chile did occasion a substantial research effort into both selective breeding for resistance and genetic engineering to confer resistance, but the level of shoot moth damage has naturally abated to tolerable levels (Lanfranco et al. 1991).

Mininco radiata breeders have put strong emphasis on managing the breeding population, and have been relying on both sexually and vegetatively propagated stock for operational planting. Related research, by Sergio Espinoza and colleagues (Espinoza et al. 2014, 2016) has been directed at identifying the extent and detailed basis of adaptation of intensively cultivated radiata stocks to contrasting local environments. Results to date have come from nursery-based studies, with more definitive results from field-based research still pending.

Arauco breeders and silviculturists have been more aggressively pursuing clonal deployment (C. Balocchi, pers. comm. 2014), testing large numbers of clones and deploying around 100, largely in monoclonal blocks of typically 20–40 ha. Despite work on embryogenesis, individual clones have been mass-propagated commercially for only 4–5 years, largely on account of continued maturation which costs a bit over 20% of potential gain through failure to mass-propagate all clones successfully. Because of this, and the opportunities for progressive genetic improvement over generations, a new generation of clones is now being used. Deployment is regionalised, with eight “breeding regions,” given the spread of latitude (36–41°S) and rainfall in their forest estate, with very imperfect cross-correlation of individual clonal performance between some of these growing regions. Up till 2014, a total of 534 individual clonal trials had been established. The deployment of identified clones has risen from 6% in 2008 to 27% in 2009 and nearly 90% in 3013.

7.4.4 South Africa

There the radiata breeding programme was overhauled and re-sized (John Mather pers. comm. 2011), amid numerous institutional changes involving R&D

(Liebenberg et al. 2004). Camcore, a North Carolina-based forest genetics and breeding organisation, was engaged to revise the breeding and deployment strategies. As at October 2011, 240 3rd-generation selections have been made, of which the top 30 clones have been established in a seed orchard. All of those orchard clones are subject to screening for pitch canker resistance by the Tree Protection Cooperative Programme. Orchard seed production is supplemented by some vegetative multiplication as nursery cuttings (http://www.capepine.co.za 2012).

7.4.5 Spain

The operational breeding programme in the Basque Autonomous Region had been faltering since around 2006, and effectively halted around 2010, for want of funding and loss of personnel. With the extremely fragmented ownership of radiata plantation, and the plantation holdings often a secondary commercial activity for owners, the individual owners have not been ready to pay any extra for genetically superior planting stock, and none were willing to provide suitable land for field genetic trials. Moreover, with pitch canker new planting largely ceased. So political support for the breeding programme has lapsed. In that region, however, some biotechnological research on radiata has proceeded, mainly led by Paloma Moncaleán. That research is partly based on adapting propagational technology from New Zealand (e.g. Montalbán et al. 2012), but also includes basic physiological and genomic research on radiata and some of its hybrids (e.g. De Diego et al. 2013). In the Galicia Region, however, a classical field-based radiata breeding programme has continued, along with research on the field progeny trials (e.g. Codesido and Fernández-López 2009).

7.5 Demonstration and Marketing of Genetic Gain

7.5.1 Gain

As the breeding programme advanced it has become more important to quantify the genetic merit of improved material. This involves two levels:

- individual candidates, for a range of traits, first for selection and then for offering to clients who might want to make their own choices of seed-orchard parents or else of clones for mass-deployment in clonal forestry
- crop-level performance of improved seedlots or even clones, as a more rigorous measure of achieved genetic gain.

Competitive interactions, of the sort that can occur among progenies in progeny tests or between clones in clonal tests, mean that gains in crop-level growth are likely to be less than the apparent gains at the level of the individual. Research on this aspect, however, has been limited with radiata in recent years.

7.5.1.1 Individual-Tree Performance

For practical reasons, the performance of large numbers of progenies or clones needs to be tested using small plots. The resulting efficiency of ranking the candidates, however, comes at the cost of competitive interactions being likely to inflate growth-rate differences for growth variables, notably wood volume.

For testing and ranking selection candidates, field designs have evolved, helped by the availability of vastly improved computing power. Complete block replicates in forest-tree trials tend to be so large that they cannot partition off environmental variation at all efficiently. Small block units, as in incomplete block designs, which include alpha-designs (Williams and Matheson 1994), allow better partitioning off of environmental effects. Moreover, with the lower replication needed for testing clones, the loss of direct comparisons among subsets of candidates as in the sets-in-replicates design used in New Zealand becomes much more important.

Actually, it is possible to compensate for sub-optimal field designs, as often exist historically, by using spatial analysis (White et al. 2007, p. 430). Such analysis uses the data to estimate and correct for local environmental effects, in order to obtain the best available information on selection candidates. While that usually requires major computing power, it is now far less of a limiting factor, to the extent that spatial analysis is often a routine part of analysing field data.

7.5.1.2 Crop-Level Gains

Such gains are relatively difficult to demonstrate rigorously. Indeed, incautious interpretation of progeny- or clonal test results can lead to gross overestimates of crop-level gains, as has recently been demonstrated for eucalypt clones (Stanger et al. 2011). However, thanks to the large-plot genetic gain trials that were first planted in 1978, insights could be achieved into crop-level genetic gains in radiata. Carson et al. (1999) showed substantial genetic gains for stem volume, and that they did not trail off greatly as the trees got older and competition had longer to operate. For a conventional open-pollinated seed-orchard lot (GF improvement rating 14) the observed gain in stem volume per hectare over “climbing select” (GF7) was 17% at age 15, and projected to 13% at age 30 and 12% at age 40; for a pair-cross (GF22) the corresponding figures were 28%, 22% and 20%. Interestingly, the gains were expressed much more strongly in the sectional area per hectare than in tree height, whereas the expectation had been that gains in wood volume would be driven by gains in height growth. However, the influence of the trade-off between wood density and stem volume in these stem-volume gains was not studied. The gains in growth were of course accompanied by major gains in the standard of tree form.

Since then, advances in knowledge of crop-level gains in wood volume production have been hampered by limited planting of large-plot genetic gain trials.

Even so, Kimberley et al. (2015) have confirmed that genetic gains in wood volume production in radiata were well sustained as the trees got older, were closely related to Improvement Rating, and varied little percentagewise among sites of varying productivity.

7.5.2 Certification and Assurance

7.5.2.1 New Zealand

The New Zealand certification scheme for genetic quality of radiata was brought under Registered Trademark as *GFPlus* in 1998. The ratings for Growth and Form continued, based mainly on progeny-test performance of the parents of the seedlots. This, however, became complicated by shifts over time in the emphasis given to different traits. With some higher GF ratings, which reflected more intensive selection for tree form, additional gains in growth rate were not always evident, especially when there was an element of selection for increased wood density or even better stiffness.

Underpinning the improvement ratings, or to some degree supplementing them, came estimates of genetic merit of the individual parents, in the form of breeding values. Adapting practice in animal breeding, using BLUP (Best Linear Unbiased Prediction) software, this was designed to cope with parents—and offspring—belonging to different generations and either different lineages or varying relatedness, and with varying levels of representation in field tests. First adopted in 1998 (Jayawickrama and Carson 1990), such estimates could behave erratically, depending on the level of cross-reference between field trials and the availability of new assessment data. Such estimates were on a trait-by-trait basis. They were also made without addressing genotype-site interaction, although this is often a minor limitation in New Zealand (Carson 1991).

Despite limited new planting, and the option of vegetative multiplication, the requirements for restocking of felled areas sustained a strong demand for genetically superior seed. Even so, substantial seed exports were made to northern Spain, where retirement of marginal land was leading to much afforestation.

7.5.2.2 Australia

In Australia, the Improvement Ratings embedded in the New Zealand certification scheme were never formally adopted. Instead, TREEPLAN was used from the outset, from 2002, to give explicit estimates of breeding values, using multi-trait information. As in New Zealand, genotype-site interaction is not yet accommodated in breeding value estimates, which can be more of an issue across Australia and is recognised as posing a major challenge.

7.5.2.3 Economic Returns

The major effort on assessing economic returns has been in Australia. This has tended to be addressed indirectly, largely in connection with assigning economic weights to different traits. Rigorous quantification of economic returns is complicated by a number of factors:

- difficulties in tracking all costs associated with genetic improvement programmes; the total costs include ones incurred by parties other than the actual breeders, and the costs of approaches that eventually fail in a process of trial and error
- continuing uncertainties over relative economic weights of different traits
- market imperfections, whereby trading prices may not reflect true value, a situation indicated by different sets of economic weights for growers and processors respectively
- unquantified payoffs, such as cheaper and safer harvesting and retention of competitive viability in industry enterprises
- shortage of recent field trials that show genetic gains at whole-crop level; especially as comparisons among operational stands representing different levels of genetic improvement have given equivocal results
- continuing uncertainties as to how certain trade-offs, notably between wood density and stem volume at the whole-crop level, play out at harvest age
- changes in practices, such as setting harvest ages, which can change the relative economic weights of different traits
- wide variation among site categories and among industry members in relative economic weights of different traits.

Claims for economic rates of return have varied widely. After in-house tracking of the cumulative historical costs of New Zealand's radiata breeding programme, and studying results of early genetic gain trials, an estimated benefit-cost ratio for radiata breeding of 46: 1 was arrived at, but a later in-house study gave an estimate of only 14: 1. Various other figures for economic benefits have been produced (e.g. Wu et al. 2007a), albeit not to any common criterion.

There was no doubt about early imperatives to improve tree form and/or adaptation to local conditions, according to different regions where radiata is grown, although much could be achieved over time by a combination of semi-natural and silvicultural selection. Intensive breeding has produced material that is strongly and unreservedly preferred by forest growers, who are typically prepared to pay extra for it. Nowadays, the immediate imperative is to improve wood properties, to maintain commercial competitiveness of both growers and processors. For the longer term, there remains the imperative to prepare for changes in breeding goals, which may come abruptly, if there is a biotic crisis to address. Unfortunately, the attractions of growing genetically improved forest crops can create strong disincentives to prepare for unexpected future developments.

7.6 Advances in Knowledge of Genetic Architecture

7.6.1 Variation among Natural Populations

Main advances have come from catch-up work in Australia, where some quite old provenance trials from the 1978 seed collection have been assessed recently (Gapare et al. 2012a,b). Among the native provenances, Año Nuevo has tended to perform best on moist, relatively fertile sites. On drier, less fertile sites Monterey has tended to do slightly better than Año Nuevo, whereas Cambria has done relatively well on some dry sites. Cambria and the Island populations have tended to perform poorly on moist, summer rainfall sites where dothistroma needle blight is a hazard (Gapare et al. 2012a). Any advantage the Cedros provenance may have for hot, dry sites has tended to be negated by susceptibility to post-planting mortality. Wood properties have generally compared among the provenances much the same as they have in New Zealand. However, Cedros has not shown superior wood stiffness commensurate with its superiority for wood density, unlike Guadalupe (Gapare et al. 2012b).

7.6.2 Within-Population Variation and Inheritance

Updated information on the variability and inheritance of individual traits in radiata is summarised in Table 7.4.

7.6.2.1 Wood Properties

Concerns over wood properties of radiata have centred on several problems: poor stiffness (Modulus of Elasticity, or MoE) affecting structural grades; dimensional instability in service which affects both structural and appearance grades; and some features affecting appearance grades, namely resin pockets, bird's-eye grain and internal checking during drying. Density had been assumed to be the main determinant of stiffness, which it is in the outerwood. However, in the corewood, which represents a substantial proportion of stem volume unless trees are beyond any commercially accepted harvest age, there is another important determinant of stiffness, namely microfibril angle (MfA), the inclination of the smallest-scale cellulose strands from the fibre axis. MfA being difficult to determine cheaply, MoE needs to be addressed in its own right; even so, it is now usually addressed through a proxy in the form of acoustic properties of the wood. Among the other problems with wood properties, especially in corewood, dimensional stability is governed by both spirality of the wood grain and uneven longitudinal shrinkage (LS) upon drying, both of which are most marked in corewood. Indeed, poor MoE

Table 7.4 General importance and indicative information obtained since around 1990 on variability and heritability of selected individual traits in radiata pine (Mainly after Wu et al. 2008, Kumar et al. 2008 and Mead 2013 and sources)

Trait	Economic importance	Status[a]	Coefficient of variation (%)[b]	Heritability	Importance of	
					Non-additive gene effects	Genotype-site interaction
Wood stiffness	Very high	BG	~10	0.6	•	•
Acoustic velocity	Indirect	Sel	10	0.4	••	•
Microfibril angle	Indirect	Inc	10	~0.6	◦?	◦
Wood collapse	High −ve	Sp	~40	0.2	•••?	?•
Longitudinal shrinkage (−ve)	High −ve	Sp	~40	0.3	•••	?
Resin pockets	Locally −ve	Sp	–	–	?	?
External resin bleeding	Indirect	Sel	≥50	0.3–0.4	•	?
Resistance to						
Mg deficiency	Uncertain	No	–	0.7	?	?
Pitch canker	Locally high	Sp	–	~0.4	?	?
Essigella	Locally high	Sp	–	0.4	•	•

[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 to date in breeding

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

has been associated with LS (Ivković et al. 2009), the former being appreciably heritable (Gapare et al. 2008). Internal checking, which occurs during drying, only becomes evident after wood is planed smooth, and affects appearance badly; while generally affecting corewood, it does not affect the wood after it becomes heartwood. Heartwood, however, can be objectionable because of its appearance and difficulty of preservative treatment. Resin pockets, while of no real consequence for structural timber can cause serious losses of potentially high-value appearance grades, while bird's-eye grain almost exclusively affects corewood and in radiata is viewed by the market as a defect rather than an attribute.

Obtaining good knowledge of inheritance of traits, just like being able to select intensively, depends on being able to evaluate large numbers of individuals. This in turn depends on cheap and reasonably accurate assay technologies, for either the actual traits of interest or reliable proxies. This posed special challenges with wood-property traits (Sect. 7.7.1), especially ones that affect wood quality more directly. Stiffness can now be assayed on standing trees at reasonable cost, using proprietary instruments such as TreeTap and FAKOPP. Susceptibility to internal checking, which results from fibre collapse during drying because of cohesiveness of capillary water columns, has been very challenging to assay. It is partly associated with low wood density, so can be reduced by selecting for high wood density, but high wood density is not generally needed for appearance grades. A rough assay, however, can be obtained by measuring tangential shrinkage when increment cores dry rapidly. Such a measure of susceptibility to collapse has shown strong broad-sense heritability but only low narrow-sense heritability (Kumar et al. 2008), suggesting considerable non-additive gene effects. Indeed, some heritability has been demonstrated for actual incidence of internal checking (Kumar et al. 2010). Incidence of resin pockets is indicated, albeit far from precisely, by external resin bleeding (Cown et al. 2011).

Stiffness has shown significant heritability in its own right (e.g. Dungey et al. 2006; Baltunis et al. 2007; Matheson et al. 2008; Kumar and Burdon 2010; Gapare et al. 2012b) but is less heritable and more subject to genotype-site interaction than wood density. The general picture appears to be one of performance-related wood properties to be less heritable and more subject to non-additive inheritance than wood density, especially in the corewood (Kumar et al. 2008).

Pilot work has been done to develop very early screening for wood density, stiffness (as acoustic velocity), and shrinkage behaviour (which governs dimensional stability), by forcing young seedlings out of the vertical to study the development and properties of the resulting wood (Apiolaza et al. 2011). Modest heritabilities were observed for these variables; however, a very strong and favourable genetic correlation was observed between velocity and shrinkage, but in the opposite wood rather than in the induced compression wood. The value of the results will depend on genetic correlations with later performance of the trees.

7.6.2.2 Uncomfortable Trade-Offs

With very few exceptions, wood properties have exhibited varyingly adverse genetic correlations with growth variables (Kumar et al. 2008; Wu et al. 2008; Gapare et al. 2009; Burdon 2010) (Table 7.5). Typically, these correlations have been more adverse with stem diameter than with height; moreover, because of the contribution of the square of diameter to stem volume, and the coefficients of variation (standard deviations divided by the means) for height and diameter, the genetic correlations of diameter and stem volume with other traits are often almost identical. Adverse genetic correlations between economically important traits make life particularly difficult for the breeder, for several reasons. They can constrain attainable breeding goals, in terms of gains simultaneously obtainable in the traits concerned (Sect. 4.3.2). They also mean that the breeder needs good information on comparative economic weights; otherwise, effective selection can actually reduce economic value. Moreover, with wood properties, especially density, it becomes a matter of having to weigh up the wood properties versus stem volume measurements in selecting quite young trees (Burdon 2010). That is fine for the

Table 7.5 Approximate pattern, in terms of sign and strength, of genetic correlations between traits. Pluses denote positive or favourable correlations, minuses negative or adverse correlations, 0 roughly neutral (Adapted from Burdon (1992) and Wu et al. (2008))

	HT	DIAM	BRF	IL	BDA	STR	DEN	STF	STA
Height (HT)	1								
Stem diameter (DIAM)	+++	1							
Branching frequency (BRF)	+*	++*	1						
Internode length (IL)	(–)	(–)	(– –)						
Branch diam./angle (BDA)	–	+	++	(– –)	1				
Stem straightness (STR)	++	+	+	(–)	++	1			
Wood density (DEN)	–	–	0	(0)	0	0	1		
Wood stiffness (STF)	(–)	–	0	(0)	0	0	++	1	
Dimensional stability (STA)	(–)	(–)	(0)	(0)	(–)	(0)	(0)	(++)	1

*Much less pronounced on slower-growth sites

Parentheses indicate evidence is indirect or sketchy (Sect. 7.6.2)

wood properties, which are most problematic when the trees are young, but the volume production that matters is at final harvest, and the projection of early, single-tree volumes to crop performance at final harvest is basically guesswork, the more so because of the genetic trade-offs.

7.6.2.3 Other Aspects

With new diseases having appeared, tree-to-tree variation and heritability of resistance is of much interest. For pitch canker, length of lesions in inoculated seedlings showed a narrow-sense heritability of ca. 0.4 (Matheson et al. 2006), although it is not known how good a proxy the response is for field resistance. Heritabilities of resistance to *P. pinifolia* and RNC are now being researched in Chile and New Zealand respectively.

Selecting trees while young can give more rapid genetic gain, provided the early-age trait shows both satisfactory heritability and adequate genetic correlation with the mature-age trait—in addition to being able to evaluate enough individuals. The two traits can be the same at different ages, but they do not have to be, provided the above conditions are met. If extremely early selection is effective, it might be applied to shortlist the candidates that are subjected to further evaluation, as in field tests.

A pattern of age-age genetic correlations had already been established for growth variables in radiata, whereby selection at about one-third the harvest age is efficient in terms of gain per unit time, even if markedly suboptimal in gain per generation. With wood properties, as with resistance to certain diseases, the expression of traits at quite early ages can actually be of direct economic importance.

Even so, interest exists in extremely early evaluation. This requires at least reasonable heritabilities at a very early age, combined with worthwhile age-age genetic correlations, conditions that have generally not been demonstrated. On the other hand, wood properties in quite young trees, around 6–7 years old, are of interest in their own right since they involve the troublesome corewood (e.g. Wu et al. 2007b), while trees that are younger cannot generally be used for intermating in any population.

7.6.3 Genotype-Environment Interaction

Genotype-environment interaction has often been prevalent for radiata in Australia, and yet it has largely defied efforts to discern any pattern (e.g. Matheson and Raymond 1984; Cullis et al. 2015). Historically, phosphorus deficiency has implicated as a driver of interactions (Fielding and Brown 1961; Burdon 1975; Burdon et al. 1997a,b, 1998), but correction of this deficiency by using fertiliser has now become routine. Occasional exceptions have arisen when specific maladaptations of individual clones or families have been exposed on particular sites. Recent work, however, has revealed a pattern of interactions in New South Wales (Raymond 2011; Gapare et al. 2012a), in that performance on moist, high-altitude sites correlated quite poorly with performance on dry, low-altitude sites. The detailed basis for such a pattern of interaction, however, is unclear. A general problem in both New Zealand and Australia was limited overlap between field trials in representation of progenies (Raymond 2011; Apiolaza 2012; Gapare et al. 2012b, Cullis et al. 2015).

As in past studies, diameter growth appeared to be the trait that showed the most interaction. In some cases, there were obvious causes, such as disease-prone parents being differentially affected among sites of widely varying disease hazard, but such obvious causes were not always evident. Tree-form traits, notably branching pattern, tended to be less subject to interaction, while certain wood properties, notably density, often showed minimal interaction, with rankings varying very little among sites (Apiolaza 2012). However, some wood properties of major practical interest, such as stiffness or shrinkage behaviour upon drying, could show quite marked interaction, although those interactions may involve different levels of expression of genetic variation rather than changes of genotypic rankings.

7.6.4 Performance of Species Hybrids

The one easily produced species hybrid of radiata, with the knobcone pine (*Pinus attenuata*) (Fig. 7.4), has been tested on a small scale in New Zealand over many years. On many sites it had too much of knobcone pine's susceptibility to dothistroma needle blight to warrant any consideration. However, it continued to show

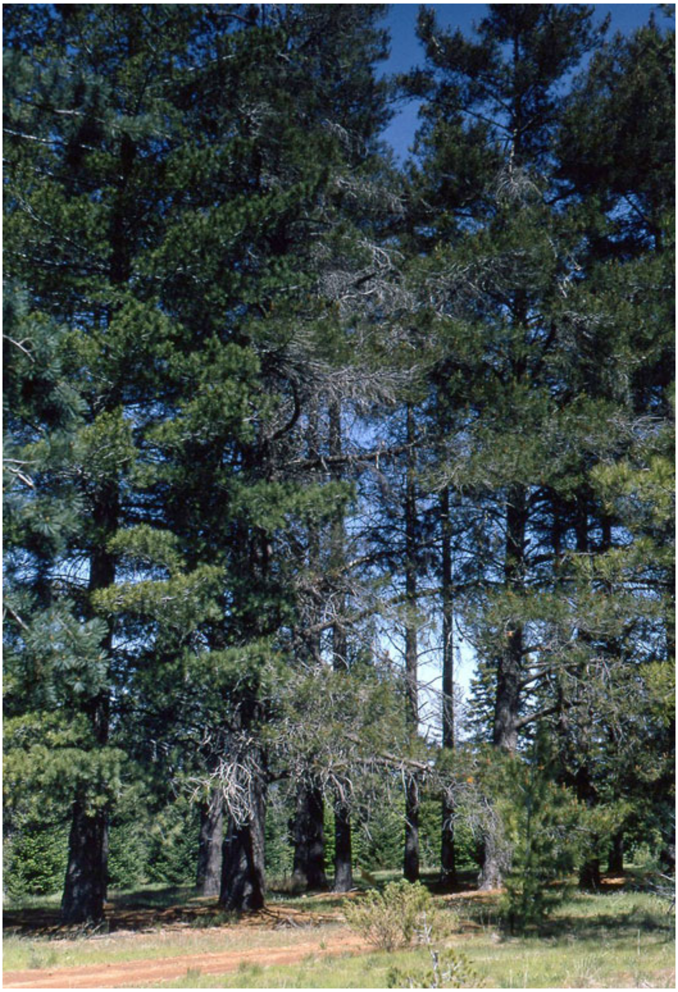

Fig. 7.4 Hybrids between radiata and knobcone pines, combining almost the full growth potential of radiata with much superior resistance to snow damage; as such they promise an effective extension of the site tolerances of radiata, but are not an option where dothistroma blight can be a factor (Photo RDB)

promise in the semi-continental climates of central South Island, where dothistroma is not a factor, but frost, drought and snowfalls pose problems for radiata. Over the years, the hybrid appeared better adapted to these harsh sites, but a revelation came in 2006 (Dungey et al. 2011), following a heavy fall of wet snow in an 8-year-old hybrid trial. On two harsh sites, the hybrids, which had outgrown the knobcone parent and kept up well with radiata, showed to full advantage. The snow caused severe damage in the pure radiata, compared with almost none in knobcone and very little in the hybrids. In a separate trial, on a harsh, droughty site, hybrids of knobcone and Cedros Island radiata have been showing special promise (N.J. Ledgard unpubl.); intriguingly, this was despite the site being boron-deficient and the pure Cedros provenance being prone to this deficiency. Anecdotal observations (RDB and WJL 2001) of a planting of the radiata and knobcone hybrid combination in northern Sierra Nevada, California, have shown the same great superiority for snow resistance in the hybrids compared with radiata.

The hybrids' tolerance of snow and cold, and presumably drought, effectively mean a substantial extension of the areas where radiata can be grown safely. Actually, no current demand exists for planting hybrids on such semi-continental sites, even though such sites can be very productive on account of some good soils, good rainfall and abundant sunshine. Moreover, the hybrids are not expected to share the unwelcome invasiveness of various exotic conifers in central South Island, New Zealand.

Other interspecific hybrids are of interest (Dungey et al. 2003), especially ones with Mexican pines of the closely related subsection of *Pinus*, the Oocarpae. These species, coming from summer-rainfall areas, can be expected to have very different spectra of disease resistance from radiata which is already grown widely in areas of known disease hazard and may be highly vulnerable to some new disease. Such pines are known to be in varying degrees more resistant to pitch canker (Hodge and Dvorak 2000). Of greatest interest has been the hybrid with *P. tecunumannii* but it has been difficult to produce and commitment of resources has been limited, although CAMCORE are giving active support to South Africa in trying to cross radiata with canker-resistant species. Easier to produce but less attractive is the hybrid with *P. greggii*.

7.7 Evolution and Differentiation of Breeding Goals

7.7.1 The Blitz on Wood Properties

From the very early days, industry parties had balked at making calls for genetic improvement of wood properties in radiata, largely because they were unwilling to contemplate any consequent sacrifice in stem volume production (Burdon 2010). Eventually, after stockings and harvest ages had been lowered, the imperative for genetic improvement of certain wood properties became clear. Indeed, operational screening of logs for wood stiffness was adopted for pricing logs and allocating them to process lines (Fig. 7.5).

Thus, by 1997 there was a strong call for genetic improvement of radiata's wood properties, in Australia as well as in New Zealand (e.g. Cave and Walker 1994; see also Sects. 6.3.2.2 and 6.7.2.4). Answering this call, however, was impeded by several factors. For properties of immediate economic interest, notably stiffness, inheritance was uncertain. While the importance of microfibril angle

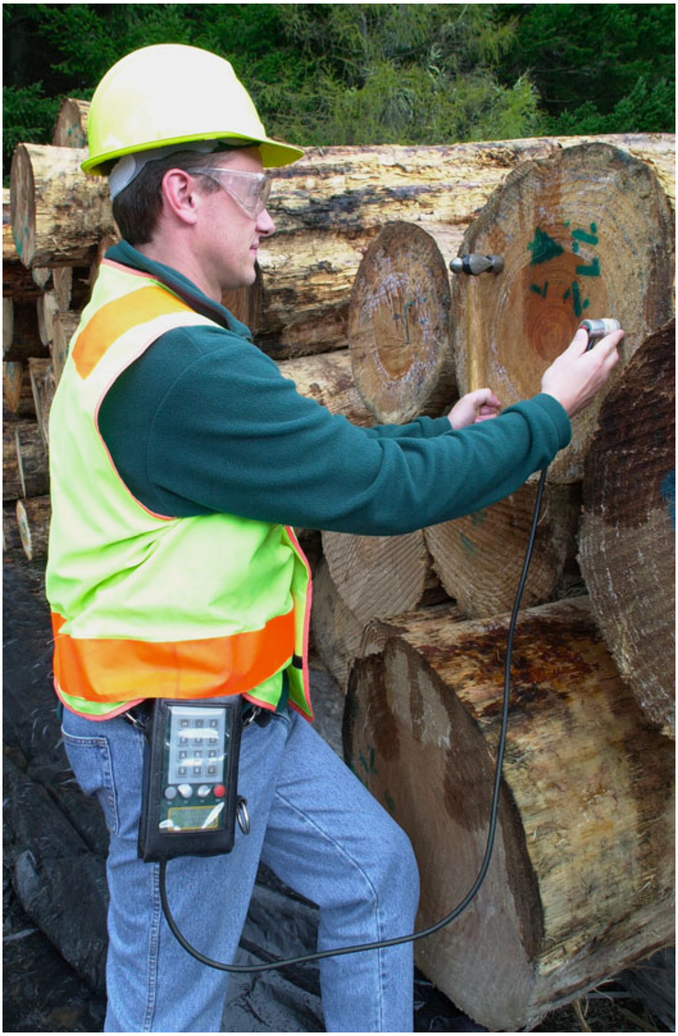

Fig. 7.5 Demonstration of using HitMan instrument for determining wood stiffness of a radiata log, as basis for log sorting

(MfA) as a determinant of stiffness especially in corewood had become increasingly clear (Butterfield et al. 1997), and there has been a technical advance in its determination (Evans 2006) the costs and difficulty of direct operational assays of selection candidates for MfA have remained effectively prohibitive. Whether the heritability of stiffness as such was high enough to justify seeking genetic improvement, except purely through selection for density, was not fully clear. Also uncertain was the magnitude of adverse genetic correlations with growth rate. The roles of basic properties in influencing product-performance properties, such as dimensional stability of sawn timber in service were not always clear.

Moreover, uncertainty as to the economic importance of wood properties relative to that of volume growth, along with uncertain genetic correlations, meant the two key classes of information were missing for being able to define realistic breeding goals and assure positive economic gain from selection. Furthermore, the direct assay technology for evaluating selection candidates was expensive or unreliable or both, while reliable and easily determined proxy traits often remained to be confirmed.

Since then, assay technology has improved radically, and various proxies for quality-related traits have been confirmed, which have allowed both greater selection intensities for wood quality and much better information on inheritance. As mentioned in Sect. 6.7.2.4, various anatomical properties and stiffness of wood can be evaluated electronically on increment cores, using the SilviScan instrument; however, cost per core and service availability are problems. Stiffness can now be measured in standing trees, using different acoustic tools (Sect. 7.6.2.1), which measure time of sound transmission between two points on the lower bole. To a lesser degree, progress has been made in assay technology for shrinkage properties (as a proxy for dimensional stability) and resin pockets. Grain spirality, which also affects dimensional stability, has remained a difficult trait to assay, despite promising early indications of high heritability (Burdon and Low 1992: Sorensson et al. 1997). A very recent—and not fully documented—development in New Zealand is "Discbot" hardware and software for evaluating physical, chemical and anatomical wood properties, on stem cross-sectional discs. Compared with SilviScan it evaluates the entire section as opposed to individual radii, and has the additional capability of evaluating grain spirality. The destructive nature of taking discs can be mitigated by taking the discs from the ends of cut logs or by having individuals clonally replicated so a tree can be sacrificed without destroying all members of a genotype.

While the range of wood properties for which selection can be made has broadened, there remains the issue of how to weigh them up against potential improvement in other traits, especially as there are typically adverse genetic correlations between wood properties and growth traits. The main efforts to derive economic weights for different traits have been in Australia, where the focus on producing light structural timber is especially strong. In particular, a joint study by CSIRO and STBA (Ivković et al. 2006) indicated that for growers stem volume production was the most important economic trait, while for sawmillers stiffness was. Apart from the fact that the study depended on strong assumptions concerning how volume and stiffness trade off at harvest age, this divergence points to a flawed log pricing structure. In New Zealand, where there is typically a broader mix of end-products, such a study is more complicated. In Chile, the greater relative importance of pulpwood would also cause complications.

Recently Apiolaza et al. (2011) and Sharma et al. (2015) have started exploring the possibility of evaluating wood properties on extremely young trees. Trees under two years old were placed on a lean, to study compression wood formation, stiffness, and longitudinal shrinkage which mainly governs dimensional stability. Heritable variation was evident in the trees, although the practical value for selection remains to be confirmed. Such selection would likely have its main application in starting the progressive culling of clones for deployment in clonal forestry, rather than in the actual breeding population.

Meanwhile much research has been undertaken, and will continue, on trying to develop the use of DNA sequences for selecting for wood properties (Sect. 7.11.1.4).

7.7.2 Disease and Pest Resistance

While some degree of selection had become routine in New Zealand and New South Wales for resistance to dothistroma needle blight and cyclaneusma needle cast (Burdon et al. 2008), disease resistance had not been a prime concern for genetic improvement. In the last few years, however, biotic events have raised new concerns over a need to mount, at short notice, selection programmes to achieve rapid gains in disease resistance. Not only that, experience has taught that the diseases might well be hitherto unknown. This has spurred interest in cross-resistance to a range of fungal pathogens, but awaits substantial research verification, Moreover, the potential for genetic engineering to introduce several genes of large effect that collectively assure durable resistance now appears very attractive (Burdon and Wilcox 2011), provided such genes can be identified. The identification will remain a challenge for some time to come, but if it is achieved the prospects are now very good for being able to insert such genes by transformation (the favoured form of genetic engineering).

A very proactive move was testing Australian and New Zealand select material in California for resistance to pitch canker (Sect. 7.3.5), but that was unsuccessful because almost no pitch canker infection was evident with all observed dieback being attributable to infection by the long-known pathogen *Diplodia pinea*.

A new avenue for studying disease resistance has opened up in recent years, involving endophytes, which are fungi that live harmlessly or even beneficially in the tissues of plants. Endophytes are actually remarkably prevalent in conifers (e.g. Ganley and Newcombe 2006), and manipulating endophyte populations, if achievable, may confer protection against a range of pathogens (Eyles et al. 2010).

7.7.3 Specialisation or Not, and Deployment

A perennial debate has continued over whether, in the presence of substantial genotype-environment interaction, to select parents or clones for specific conditions or for a broad range of conditions. Either approach, however, depends on good knowledge of the patterns of interaction, in terms of what environmental factors drive interaction. For specialised selection this means being able to define site categories within which interaction may be minor. For selecting broadly adapted genotypes, one wants to be able to define an environment, or a small set of environments, where good performance can guarantee broad adaptation (Li et al. 2017).

Actually, specialisation of selections for sites may be indicated in the absence of any interaction. For several traits, radiata shows massive environmental effects. According to site types, wood properties may or may not be severely limiting. On many cold but fertile sites, wood density and stiffness tend to be too low in radiata for structural timber grades. There, one could either select intensively for density and/or stiffness, at the expense of genetic gain in some other traits, or else one could focus on producing appearance grades which would require different tending regimes if not a separate "breed."

Actually, significant selection on a "horses-for-courses" basis can be done without having formally differentiated breeds. Even within a breed, genetic segregation will guarantee considerable variation among individual offspring. For field deployment, therefore, a customer can choose individually the parents for a seed orchard (and/or mass vegetative multiplication of seedlings) or clones for direct vegetative propagation. For choosing orchard parents on this basis, good estimates of breeding values are paramount; likewise with genotypic values for deployment in clonal forestry.

7.8 Strategy and Management of Total Genetic Resources

7.8.1 Native-Population Resources (CONSERVE)

Large plantings had been made from the 1978 seed collections in the natural stands, to establish both numerous provenance trials and gene-resource blocks. In Australia, these plantings were mainly provenance trials, with smaller numbers but larger areas of gene-resource plantings which, together with some earlier trials, brought the total to 67 provenance plantings (Eldridge 1998). In New Zealand, provenance trials from that collection numbered 23; these were complemented by larger, gene-resource plantings which covered a total of 135 ha between eight other sites. Together with earlier provenance trials these plantings from the 1978 collection brought the total up to 47 provenance plantings in New Zealand (Eldridge 1998).

Provenance trials had been assessed more or less systematically in New Zealand, the aim being to assess them at comparable tree heights, such that almost all were assessed by age 12 from planting. Only one trial rated as an outright failure, although several others were a limited success. Some were reassessed at age 15, mainly confirming earlier comparisons. In addition to being the subject of the formal provenance trials, native-provenance seedlots were included as ancillary material in various progeny trials involving breeding-population material. Overall, a clear picture emerged of the adaptive profiles of the various provenances in relation to New Zealand conditions (Burdon et al. 1997a, 1998 – also Sect. 6.7.1.1).

In Australia, some trials were assessed quite promptly, and an early picture emerged of tolerances of salinity and of the root pathogen *Phytophthora cinnamomi* (Sect. 6.7.1.2). Many other trials, however, were largely neglected, and some were lost to disasters, generally fire; the latter fate was shared by some of the gene-resource plantings. Nevertheless, a picture has eventually emerged of adaptive profiles of provenances relative to Australian conditions.

In both countries, the performance of the native-population collections for both growth rate and tree form tended to be substantially inferior to that of intensively select breeding-population seedlots. This was no surprise for breeders; indeed, it was a further vindication of their efforts. Industry parties, however, having less of a focus on the cryptic variation that might be needed in future circumstances, were put off by the indifferent performance of fully wild material, such that both the RPBC and the STBA were very reluctant to commit time and money to maintaining and renewing these gene resources. This work repeatedly appeared in the proposals, only to be pushed off the end of the list of priorities. Eventually, however, a meeting was called, in the form of the CONSERVE Workshop held in Canberra in 1998 (Matheson et al. 1999). The following principles were agreed on:

- reliance on open pollination to perpetuate the collections
- planting large blocks (≥20 ha, effective population ≥2000) per subpopulation, or else replicating between sites
- rotations extended as long as possible
- priority to care of Cambria among mainland populations
- Guadalupe population in hand, with recent new conservation plantings
- stored seed from Cedros to be sown for planting.

A few plus trees from mainland provenance material in New Zealand had been selected and archived in 1986, along with 47 from the Guadalupe provenance. Then in 1994, further plus trees were selected, almost all in gene-resource plantings from the Californian mainland. In New Zealand, 37, 57 and 34 trees were selected from within the Año Nuevo, Monterey and Cambria provenances respectively (Bian et al. 2011), and open-pollinated seed collected, while a few of the seed parents have since been archived as clones. Some "secondary" provenance trials have since established from these seed collections, but results to date have added little to the existing picture of provenance differences. In the last four years, in the course of felling, a further seed collection of open-pollinated seed has been made, generally from 40 or so of the better trees in each of the 13 subdivisions of the mainland populations. The seed is in storage, with a separate lot for each seed parent, with a view to eventually re-establishing the gene resources as proposed in Shelbourne et al. (1986).

Overall, commitment to maintaining large genetic resources of native-population material has been limited. The gap in genotypic merit between wild and domesticated material is increasing the opportunity costs of maintaining wild material, and thence the reluctance to grow it. Yet large stocks of wild material would be needed to give scope for the very intensive selection that would be needed to mitigate that gap. And there have been no serious efforts to generate the large, complex interpopulation hybrid swarms that would expose the full range of potential gene combinations to intensive natural and artificial selection. The institutional resistance, or inertia, has doubtless been accentuated by varying combinations of rapid changes in forest ownership and a widespread short-term commercial focus.

Meanwhile, the advent of pitch canker in California, and the consequent biosecurity concerns, have placed native stands off limits for further gene-resource imports into Australia and New Zealand.

7.8.2 Structuring of Breeding Populations

In both New Zealand and Australia the breeding plans, based upon the structuring of the breeding populations, have been significantly revised.

7.8.2.1 Australia

The STBA came up with a new breeding plan (White et al (1999), which superseded that adopted in 1993 (Boomsma 1997), and which has undergone some further evolution (Wu et al. 2007a). Developments include

- dropping the stratification, adopted in 1993, into the Nucleus and Main populations
- retention of two unrelated sublines to guarantee future outcrossing
- adoption of the "rolling front" feature (Borralho and Dutkowski 1998) in place of discrete generations, to smooth the workload and accelerate the capture of genetic gain
- interim maintenance of the three-breed structure of the breeding population, but eventual relegation of the breeds structure to the level of field-deployed crops
- reduction of population size to a census number of 340
- planned infusion of new genetic material in selections from the 1978 seed collections made in the natural populations.

Underpinning both the management of genetic material and the marketing of seed or planting stock has been the system of calculating estimated, or "predicted" breeding values of individual members of the population for various traits, using the TREEPLAN® software of PlantPlan Genetics Pty Ltd.

An ancillary feature has been a small side programme that embraced deliberate use of quite intense inbreeding (Wu et al. 2004 and preceding papers in the series). Two generations of inbreeding were practised, which ranged in intensity from matings between half-sibs to two generations of selfing. Inbreeding depression was evident, but with widely different responses among lineages to increased inbreeding. While optimism has been expressed over the prospects of inbreeding to "purge" inbreeding depression in radiata (Wu et al. 2004), this approach involves additional costs and wastage of genetic material, and is not being adopted operationally.

7.8.2.2 New Zealand

A strategy review of the radiata breeding programme had been undertaken in 1990 (Jayawickrama and Carson 1990). It reaffirmed the adoption of subdividing the breeding population into just two unrelated sublines, a feature that that was incorporated soon after the production of the 1986 Breeding Plan (Shelbourne et al. 1986). It adopted the stratification of the breeding population into the elite Nucleus and the Main components, but specialised breeds (Structural Timber and Clear Cuttings) were designated as components of the Nucleus, along with the top-ranking Growth and Form component. The lower-rated Main was not differentiated into breeds. Controlled pair-crossing was planned throughout. A separate pair-crossed breeding population was to be maintained for the Guadalupe provenance, based on 67 plus-tree selections made among New Zealand plantings. Numbers of parents envisaged per generation were 225 for the Main population, plus 24 from each of two specialised breeds.

Further revision of the strategy for the breeding population came from a review begun in 2004 and essentially completed in 2007 (Dungey et al. 2009). Features of this included:

- retaining the two-subline structure (Red and White “superlines”)
- testing the two superlines on disjunct sites
- 250 parents per subline
- retaining the differentiation into Elite and Main strata
- 24 parents per subline within the elite
- dropping of the specialised breed designation (although the breed differentiation would not be extinguished immediately)
- Dropping of controlled crossing in main population, in favour of open pollination, in expectation that pedigree reconstruction will become feasible
- retention of controlled double-pair crossing in the Elite stratum
- testing of Elite progenies on 10 sites (five per superline)
- clonal replication within Elite offspring (20 clones × 2 cuttings × 5 sites)
- supplementing these clones with seedlings in the Elite
- testing of Main progenies on eight sites (four per superline)
- 20 seedlings per family per site in Main.

In addition, the separate pure Guadalupe breeding population, based on 67 parents, was left to stand. So, too, was a pure Cedros breeding population, based on 30 parents, which had been put in place since the 1990 review.

The proposal for clonal replication of individual offspring was controversial, hence its adoption for only part of the Elite stratum.

7.8.2.3 Chile

In keeping with the structure of the breeding Cooperativa, company breeding programmes have tended to remain largely self-contained, with the actual breeding continuing largely along the originally planned lines. Despite the widespread success of seed orchards, vegetative multiplication has been vigorously adopted in some quarters to speed up the operational capture of genetic gain (e.g. Balocchi 1997).

Genetic resistance to the pine shoot moth has been explored, even enlisting New Zealand researchers to confer it by genetic engineering (Grace et al. 2005), but the single resistant transgenic cell line was not put into operational use.

7.9 Advances and Problems in Propagation Technology

7.9.1 Vegetative Propagation

7.9.1.1 Advances

Producing cuttings of radiata for vegetative multiplication of scarce seedlots was by 1998 a reasonably "mature technology." So too was production of radiata plantlets using in-vitro culture for rapid initial multiplication. Neither technology, however, could actually beat the process of maturation and the problems it posed. For control of maturation, and convenient storage of live clones, cryopreservation at ultra-low temperatures was already being developed for radiata (Hargreaves et al. 1997, 1999). Quite soon, it became broadly feasible, in that the various types of in-vitro cultures, namely embryos, cotyledons and shoot-tip meristems, can all be revived after removal from cryogenic storage (Hargreaves and Menzies 2007). However, embryogenesis (Fig. 7.6), as a platform for obtaining very high multiplication rates starting from fully juvenile material, was harder to achieve satisfactorily with radiata. Pursued since the late 1980s, starting with embryos of immature seeds, it would work very well with spruces, but not with radiata. A big problem was poor "genotype capture." In many whole families it would fail. Even among the remaining families, many of the seeds could not be induced to produce embryos that could be successfully reared through into plantlets. However, a

Fig. 7.6 Embryos (white) appearing on callus tissue (brownish) cultured from embryos excised from partly developed radiata seed

major breakthrough was made in increasing genotype capture for embryo initiation (Hargreaves et al. 2009, 2011). Better timing of collection of immature cones, appropriate choice of dissection technique and, above all, a modified culture medium allowed a genotype capture rate that was no longer a significant limitation. While the finding was just for embryo initiation, this is typically the limiting step in producing plantlets.

7.9.1.2 Some Stumbles

Maturation led to a failure of the initial attempts at clonal forestry with radiata (Fig. 7.7). Although control of maturation had since become quite well understood technically, practical management of it in producing planting stock has not always succeeded. Even with hedging and serial propagation, maturation will proceed insidiously, and its impact can be underestimated. That, in combination with efforts to trim production costs, can lead to a decline in the quality of nursery stock, with weaker plants and unbalanced root systems. In turn, such deterioration in quality of planting stock exacerbates the effects of slipshod establishment practice in the field, especially on difficult sites. Such establishment practice can reflect

Fig. 7.7 Early New Zealand clonal test, with single-tree plots. Good resolution of clonal differences was obtained, but by the time the best-performing clones could be selected they could no longer be repropagated reliably and cheaply

a combination of over-zealous cost-cutting and declines in field-based skills, the latter resulting from continuing rapid changes of field personnel with casualization of the labour force. Indeed, there have been significant areas of crop failure with radiata in New Zealand, requiring replanting after several years, with other, less-affected crops still significantly compromised.

Thus, despite great advances in developing software for devising prescriptions and planning field operations, success in growing crops can be seriously compromised by injudicious cost-cutting and associated losses of on-the-ground skills.

7.9.2 Seed Production and Hybridisation

With the improvements in seed-orchard siting, the capability for accelerated seed ripening by "curing" cones, and the availability of mass vegetative multiplication of scarce seed or seedling stocks, research on routine seed production became less of a priority. However, characterising stages of seed development became an issue for vegetative multiplication by embryogenesis (Hargreaves et al. 2009), to capture reliably almost all genotypes of interest.

Another aspect of seed production is production of hybrids with other species. With radiata this is potentially of great practical importance. Very few species hybridise at all readily with it, yet there are great attractions in being able to combine its advantages with making good its biotic vulnerabilities by incorporating resistances from other species. Among other species with such resistances are a number that appear closely enough related to make the prospect of hybrids tantalising. Yet, among the mainstream institutions for breeding radiata any strong commitment to overcoming crossability barriers has tended to be given low priority.

7.10 Where to for Clonal Forestry?

Despite the advances made in vegetative propagation (Menzies and Aimers-Halliday 2005), control of maturation remained a problem. Clones had often been maintained as *in-vitro* cultures or as hedges, so as to allow continued propagation for a number of years, delaying maturation in varying degrees but never halting it. Thus, continued production of high-quality cuttings or plantlets at reasonable cost has remained more difficult, and was often failing. And, where planting stock are of indifferent quality, the margins for error in site preparation, standard of planting and follow-up weed control are greatly reduced.

The development of a reliable cryopreservation system has provided the one guarantee of clonal storage in a juvenile state, which can be used in parallel with clonal evaluation (Fig. 7.8). Such use, however, depends on setting up clonal storage prior to establishing field tests, and maintaining the storage facility, requiring careful logistical preparation. With embryogenesis, the greatly improved techniques

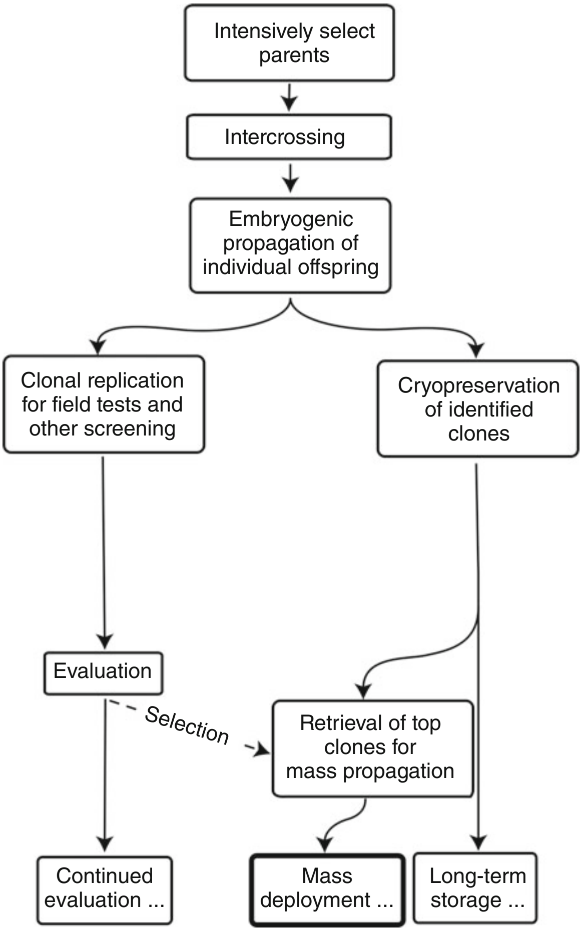

Fig. 7.8 Flow chart of operations including use of cryopreservation for storage of clones so as to halt maturation during clonal evaluation, with approximate time frame denoted in the vertical axis

(Hargreaves et al. 2009) now mean genotype capture is greatly improved and is no longer an important limitation. This avoids loss of genetic gain in the breeding objective through having to add propagability as a selection criterion, and/or a risky narrowing of the genetic base in the commercial crops.

Despite the big progress in cryogenics and embryogenesis, an ideal solution has not been achieved. That would be an ability to completely rejuvenate vegetative material of any tree at any age. This goal remains elusive, but it has never been addressed for radiata with major institutional commitment.

Even with this limitation, and some special problems of managing biotic risks (Aimers-Halliday & Burdon 2003; Burdon and Aimers-Halliday 2003), clonal forestry retains some major attractions for radiata. Outstanding clones are indeed outstanding, consistent with the expected scope for clones to capture non-additive as well as just additive genetic gain. Having logs of known wood properties, despite all the within-log variation and the technology for individual-log assay for stiffness, would still be extremely welcome. Clonal forestry offers the best prospect of precise control of branching pattern for allowing optimal recovery of clear-cuttings from unpruned trees. Moreover, monoclonal blocks offer more uniform log sizes, and they reduce the focus on competitive ability which may not totally align with crop productivity. It is thus fully understandable that vigorous pursuit of clonal forestry is proceeding in New Zealand (Sect. 7.4.2) and Chile (Sect. 7.4.3). Furthermore, clonal forestry is the context for any foreseeable operational use of genetic engineering with radiata (Burdon and Lstibůrek 2010).

While some of the advantages of clonal forestry apply to using a mosaic of monoclonal blocks, comprising enough clones for effective risk spread, the case for blocks rather than intimate mixtures of clones is not overwhelming. There may well be situations where failed clones cannot be conveniently abandoned or salvage-harvested. For deployment, clonal mixtures promise better protection against downsides of genotype-site interaction, yet, with really good knowledge, clonal forestry would allow the most effective exploitation of interaction. Certainly, clonal material offers the best information on the magnitude and patterns of interaction, because clonal trials give the highest expected “signal-to-noise” ratio.

Further evidence of similar behaviour and genetic parameters between juvenile clones and seedlings (Baltunis et al. 2009) is reassuring.

7.11 Gene Technology

7.11.1 Genomic Research

By 1998, a preliminary genomic map for radiata was available (Devey et al. 1996). There were also genomic tools for locating specific DNA sequences from another species that are present and functional in both it and another species; indeed, two or more species can be used simultaneously to attract complementary funding and provide complementary information.

However, unravelling a complete genomic sequence of a pine is a forbidding challenge. The genome is huge (at ca 2.4×10^{10} base pairs, around 10 times the size of the human genome), and the pattern of massively repeated sequences greatly exacerbates the problems of trying to arrive at a complete sequence. Hence the attractions of being able to apply genomic information from other plant species, not just pines or even other conifers, are major.

Actually, some of the very early genomic research with radiata focussed on the organelle genomes, with emphasis on chloroplasts, these genomes being much smaller than the nuclear genome and therefore more convenient to study. Advances in genomic technology and bioinformatics have since facilitated study of the nuclear genome, which is much more informative, so we do not review the studies of organelle genomes.

Among plants, the cress, *Arabidopsis thaliana*, has become the favourite model species for genomic research, because of its very small size and short lifespan, together with a very small genome. Not only can its genomic architecture be studied very easily, but effects of variant genes can be tracked through the developmental processes whereby they are expressed. Remarkably, despite very different developmental organisation, certain genes appear to be present and have similar roles in both *Arabidopsis* and pines (Krutovsky et al. 2006).

7.11.1.1 Comparative Genomics

The genomic stability of most conifers, and of pines in particular, means that much genomic information on one pine species can easily be cross-referenced (Burdon and Wilcox 2011 and references therein). By 1999, it was evident that the genomic structure of radiata and loblolly pines was very similar (Devey et al. 1999b), in terms of organisation into chromosomes, and the general arrangement of genes within chromosomes. It evidently holds for a range of pine species, if not across a wide range of conifer genera. This offers the prospect of leveraging genomic information acquired in one species for application in one or more other species. Genomic studies, however, are subject to countervailing institutional pressures. Some parties like to keep such intellectual property as proprietary information, in the face of the fact that radical advances will depend enormously on collaboration among many parties, even big ones. Against the attempts to appropriate genomic information, there are parties, notably US government agencies, that are committed to the public domain. There is in USA the Loblolly Pine Genome Project that falls within the wider Conifer Genome Project, while some other pine species, notably maritime pine (*Pinus pinaster*) and Scots pine (*Pinus sylvestris*) have also been the subject of intensive genomic studies. The scope for linking genomic research on radiata to that on other pines, especially loblolly pine, is thus considerable.

Given the pairing behaviour of DNA strands, and modern capabilities for DNA sequencing, there is now a range of techniques for locating the same or roughly homologous sequences of DNA in different species, which offers much promise of circumventing the obstacle posed by conifer genomes being too large to sequence *in toto*.

7.11.1.2 DNA Fingerprinting and Clonal Verification

For the tree breeder, it is important to be sure that identity of clonal material is correct and that pollen parentage off offspring is verified. Using the wrong clones as parents in breeding-population crosses, or in seed orchards, could lose much potential gain, the more so as a breeding programme becomes more advanced. For such fingerprinting, microsatellites, or simple sequence repeats, are DNA sequences that can be used like bar codes, as in DNA forensic work. Such sequences are non-coding DNA, characterised by variable numbers of repeats of particular short DNA base sequences. These sequences effectively show numerous alleles at a locus, such that as few as six well-chosen loci suffice to identify almost any clone (Bell et al. 2004). In fact, such fingerprinting has consistently identified misidentifications among clones in a number of tree breeding programmes, including ones involving radiata (Burdon et al. 2008). As a breeding programme progresses, eliminating such misidentifications becomes more and more important, as the genetic gains at issue increase.

Just as clonal identity needs verifying, so does both seed- and pollen-parent identity, which can be done in the same way for family seedlots.

7.11.1.3 Pedigree Reconstruction

Going one step further than verification of pollen parentage, it is in principle possible to reconstruct pedigrees. With the seed parent, this is relatively straightforward, being usually a matter of verification, with the bonus that seed megagametoyphytes (or conifer endosperm) can be used very easily for this purpose. With pollen parentage, it can be much more challenging than verifying a single pollen parent, because with open-pollinated families the potential pool of pollen parents is huge—more so with wind-pollinated species like radiata than with insect-pollinated species including eucalypts. Even so, a finite number of pollen parents may account for a high proportion of the pollinations, in which case individuals of unknowable pollen parentage might be disregarded without serious loss of genetic gain.

Indeed, the prospect of being able to reconstruct pedigrees has contributed to the acceptance in the RPBC (Dungey et al. 2009) of labour-saving open-pollination for the Main breeding population. However, much development work remains to be done before the pedigree reconstruction could be done with acceptable reliability.

7.11.1.4 Search for DNA Markers for Selection

By 1998 high hopes were held (Sect. 6.13.2) for **marker-assisted selection**^{G} (MAS) or even **marker-based selection**^{G} (MBS) for earlier and/or greater capture of genetic gain. While MAS uses genomic data in conjunction with phenotypic data, MBS uses genomic data alone and can therefore be done on younger offspring. Neither form of selection depends on identifying actual genes governing variation. Rather, they both depend on chromosomal regions containing one or a number of genes of net effect being consistently linked with one identifiable DNA marker; by ideal if improbable good luck, the marker could characterise the functional variant, being a quantitative trait nucleotide (QTN) if the marker is a single nucleotide polymorphism (SNP). Whatever the functional DNA variant(s), a chromosomal region governing expressed variation is termed a quantitative trait locus (QTL). Early theoretical work (Lande and Thompson 1990) had indicated that MAS/MBS would have the greatest advantage in situations with QTL of large effect in a context of low heritability, the problem being that proof of concept can be hardest when heritability is low. Anyway, theoretical work for a radiata breeding scenario (Wilcox et al. 2001) showed promising economic benefits from adopting MBS.

Practical development of MAS/MBS, however, encountered major problems (Burdon and Wilcox 2011). Such selection is dependent on linkage disequilibrium (LD) between the markers and the QTL, with consistent associations between particular QTL variants and particular marker alleles. But with an outbreeding species like radiata LD, while present within families, extends across populations over only minute segments of chromosomes (Kumar et al. 2003; Dillon et al. 2010). This is in sharp contrast with the situation in various crop plants which are managed as inbreeders, and to a lesser extent, the situation in dairy and poultry breeding. Even within families of radiata it can be hard to find QTL that can be reliably detected and quantified. Nominal family members can prove to be misidentified, as has happened. There was one pair-cross family that was expected to show a large QTL for wood density, and while a chromosome region was identified as a likely QTL the evidence was not conclusive (Kumar et al. 2000). Indeed, large-effect QTL appear to be very uncommon in conifers (Burdon and Wilcox 2011). Moreover, QTL of small effect are extremely difficult to detect reliably; false positives can in theory arise very easily, and reported cases of promising QTL can easily prove illusory in the light of additional data; this has all too often happened in the search for human “disease” genes.

Problems of detecting QTL in conifers have shifted research efforts in the direction of association genetics, trying to identify associations across whole outbreeding populations. In principle, this is still addressing chromosomal linkage, which may work within very small subpopulation units. In practice, however, it may largely amount to a search for SNPs that represent QTNs. That, on the face of it, is like looking for the proverbial needle in a haystack, but researchers are now looking to narrow the search by using candidate genes. These are genes that have been identified as being belonging in the developmental pathways for traits of interest, typically in plants that have already been studied in more detail. Such a study has been undertaken by Dillon et al. (2010), who tested in radiata associations between multiple variants of around 40 such genes involved in wood-forming pathways and 13 wood-core traits. A number of statistically significant associations were found, but none accounted for more than 6.5% of trait variation, although two associations were repeated in a verification population. However, scope remains for further verification, e.g. in a range of environments.

Recently, however, emphasis has shifted towards the pursuit of genomic selection (Sect. 7.2.2). This depends on cross-referencing very large numbers of genomic markers with phenotypic data (Sects. 9.2.1 and 9.3.4.4), to give global estimates of breeding values or genotypic values of candidate offspring without waiting for phenotypic information (Isik 2014). No actual reliance is placed on verifying phenotypic effects associated with specific markers. The aim is that inaccuracy of these genomic estimates can be more than compensated for by the time gained in achieving genetic advance. However, genomic markers need to be cross-referenced with phenotypic data that are an adequate guide to harvest-age performance.

7.11.1.5 Gene Expression Studies and "Gene Discovery"

Often candidate genes may be identifiable from their known roles in other plant species, leaving their roles in a species like radiata to be confirmed. Alternatively, or complementarily, "gene discovery" can be pursued directly within the subject species (Burdon and Wilcox 2011). This was done with radiata by Cato et al. (2006), studying differences in expression of genes associated with variation in wood properties among different parts of the tree, using some prior knowledge of the genes' roles. Study of expression pathways, be it to confirm roles of candidate genes or for fresh gene discovery, can involve a suite of "-'omics", i.e., transcriptomics, proteomics and metabolomics, involving the various stages of gene expression. This can be particularly important, and yet challenging, where there are alternative biochemical pathways that create redundancies, as occur in wood formation (Boudet 2000). Full confirmation of the roles of certain genes, however, may require incorporating them by genetic engineering (Sect. 7.11.2).

7.11.1.6 Some Convergence With Other Plant Breeding

Historically, forest tree breeding has aligned more closely with large animal breeding programmes, rather than with most plant breeding. The emphasis has been on progressive population improvement, rather than on producing discrete and uniform cultivar varieties. Partly because of this, and the fact that forest trees are typically outbreeders, as farm animals necessarily are, the quantitative breeding methodology used has been largely similar. A major difference among forest tree breeders and animal breeders has been that forest tree breeders readily accept that differences between sites in heritabilities can be genuine, whereas animal breeders tend to see variation in heritability estimates as reflecting sampling error about essentially constant values.

In recent years, however, the emphasis on genomic studies has in one respect narrowed the historical gap between tree breeding and most other plant breeding. On the other hand, the inbreeding systems of many domesticated crops, and the very finite population sizes of certain animal breeds, have both generated levels of linkage disequilibrium (LD) that are crucial to most marker-assisted (or marker-based) selection. By comparison, the extremely limited LD in most conifers leaves obstacles for both genomic selection and gene discovery.

7.11.2 *Genetic Engineering*

Genetic engineering (GE) has some big attractions with forest trees. It offers the prospect of introducing very specific new attributes that are not available within a species, and in quick time. Even if the attributes can be introduced by hybridisation, the process can be very slow, and crossing can bring in from the "donor" species huge numbers of unwanted genes, which can only be purged by generations of further crossing and selection. Risks, however, are involved, in possible side-effects of the process of genetic transformation and of the introduced “transgenes.” The latter are potentially catastrophic, if manifestation is delayed and risk management is not highly rigorous (Burdon and Walter 2004). Such risk management, however, can largely negate the theoretical time savings. Perceptions of the nature of the risks associated with GE vary widely among different groups of people. In fact, the major perceived risks often involve the environment (Fladung et al. 2012) rather than crop security. Research on environmental risks with GE radiata has been actively pursued (Sect. 7.11.2.2). Between risk-management considerations and ideological objections to genetic engineering—and even to any domestication of forest trees—the rule is for genetic engineering to be subject to tight regulatory protocols.

The technology for genetic transformation with radiata has advanced in that *Agrobacterium* can now be used as a vehicle for the transgenes. Selection of successfully transformed cells for regeneration of transgenic plants is achieved by incorporating resistance to a non-clinical antibiotic (traditionally kanamycin) in the transgene “construct” and using a culture medium containing that antibiotic. Advances in in-vitro culture technology have made the whole process easier. Moreover, advances in genomic technology has also made it much easier to confirm stable incorporation and actual function of particular transgenes. A recent advance, in the CRSPR technology to achieve “gene editing” (Dance 2015), is making it possible to implement genetic engineering without involving various features that were seen as either incurring certain risks or prompting ethical objections.

The basic amenability of radiata to some form of genetic engineering had been confirmed by 1998 (Walter et al. 1998). Practical demonstration of genetic engineering to confer resistance to a herbicide has been achieved in New Zealand in a tightly regulated field trial in 2013 (C. Walter et al. in prep.), despite sabotage by environmental activists who managed to breach security. Stark contrasts have been demonstrated in herbicide resistance between transformed and untransformed members of the same clones.

7.11.2.1 Target Traits

Target traits for genetic engineering of radiata have evolved. Originally, they were simply “reporter” genes that could be shown to have integrated stably into the recipient culture. Since then, the traits addressed by the New Zealand Forest Research Institute for radiata have included: herbicide resistance (Fig. 7.9); insect resistance in the *Bacterium thuringensis* (*Bt*) toxin; variants for cell-wall polymers (especially lignin); and reproductive development involving pollen production and, to a lesser extent, conelet production. Incorporation of herbicide resistance was achieved quite early (Bishop-Hurley et al. 2001), and insect resistance was also been incorporated successfully (Grace et al. 2005) albeit on only a single cell line. Achieving satisfactory reproductive sterility is more challenging, but if

Fig. 7.9 Two young plants of radiata after treatment with an effective but rapidly biodegradable herbicide: on left, killed control: on right, genetically engineered for resistance to the herbicide and unaffected (Photo Christian Walter)

achieved, it has a two-fold attraction: avoiding diversion of resources into reproduction and providing a containment mechanism for transgenes.

7.11.2.2 Associated Research

Testing for success in incorporating herbicide resistance is relatively quick and straightforward. For other, traits, however, it is more complicated. There are various ways in which genetic transformation can be used, which include inserting completely new genes or up-regulating or down-regulating existing genes. Given the complex and often redundant pathways of gene expression, up- or down-regulating genes can serve as a research tool to study the true role of particular genes. Transformation for genes governing cell wall polymers has been accompanied by culturing tissue *in vitro* to produce tracheary (wood-fibre) elements, verifying the anticipated changes in cell-wall chemistry (Wagner et al. 2007). Still to be tested, however, are the effects of such transformation of field performance and economic value of the wood (cf Wagner et al. 2009; Voelker et al. 2011). Insect resistance has been confirmed with feeding studies involving defoliating insects. The success of transformation to control reproduction will remain the subject of a relatively long-term study, done in conjunction with observing a regulatory protocol of removing all reproductive structures.

Field trials of transgenic plants have been subject to detailed study of possible environmental side-effects which have been postulated (often vehemently) by opponents of genetic engineering. Studies to date (e.g. Schnitzler 2010; Lottmann et al. 2011; Shi et al. 2012) have shown no sign of unintended, let alone adverse, environmental side-effects.

7.11.2.3 Regulatory Context

New Zealand has had the main announced commitment to genetic engineering with radiata. However, the work is done under very tight regulatory controls, in terms of the Hazardous Substances and New Organisms (HSNO) Act, which is administered by the Environmental Protection Agency (EPA), which until 2011 was called the Environmental Risk Management Authority (ERMA). The present situation mirrors the report of a Royal Commission on Genetic Modification, which sat during 2000 and reported in mid-2001. While supporting the development of the new technology, it adopted a strongly precautionary position. Approvals for genetic engineering research, when sought, are subject to public notification and submissions, with a proportion of the public implacably opposed to genetic engineering. Laboratory containment protocols are tight and field containment protocols tighter still—and almost prohibitively expensive to implement. In the interests of public transparency field trial sites are publicly identified as well as being elaborately fenced. Public notification, however, has twice led to very expensive field trials studying effectiveness and possible environmental side-effects being destroyed by environmental activists.

In Australia the political climate for genetic engineering is if anything more hostile, with states superimposing their own legislative controls over federal ones, and it has not been seriously addressed for radiata. Chile has on one occasion commissioned New Zealand researchers to attempt to introduce resistance to the European pine shoot moth, which yielded just the one individual that appeared to have been successfully transformed (Grace et al. 2005). We are not aware of any other reports of genetic engineering of radiata in Chile.

A recent court decision in New Zealand (NZHC 2014) has exposed an inadequacy in the regulatory legislation for facilitating approval of genetic modification that employs new technology to circumvent certain traditional objections.

7.12 Summary of Domestication Progress

Afforestation with radiata has lagged, and in some cases has been reversed, through a combination of factors, of which some have operated more indirectly than others. The factors include: institutional instability, international financial crises, an international boom in dairying, booms (some abortive) in afforestation with eucalypts, and neglect of environmental benefits of forestry in government policies.

Radiata gained attention for its potential to sequester carbon for combating global warming. Availability of carbon credits would reduce growing costs, especially with regimes designed to maintain wood quality, and could favour growing much bigger areas of radiata. The ways in which carbon trading and carbon liabilities have been managed in New Zealand, however, have led to deforestation rather than the expected net encouragement of the carbon sequestration.

Knowledge of inheritance patterns has continued to advance, albeit patchily. Adaptive profiles of natural populations in relation to Australian environments have become clearer. Some broad patterns of genotype-environment interactions have emerged there, but knowledge remains generally limited concerning the exact environmental factors that generate the interactions.

Emphasis has increased on genetic improvement of wood properties, with much research into targeting appropriate properties and refining assay technologies. Adverse genetic correlations between growth performance and various wood-quality traits have become better understood, and, while not always strong, tend to be pervasive. These pose major challenges for tree breeders. Ideally, breeders should become able to assign correct economic weights to adversely correlated traits. Major uncertainty concerning comparative economic weights, however, may require some alternative defensive approach(es) to guarantee gains in net economic worth. One such approach would be the pursuit of differentiated breeds, or at least differentiated deployment populations. This can accommodate different economic weights according to sites, wood-processes or end-uses, all of which can be important issues for radiata. For deployed material it also recognises that optimal values for individual traits can be conditional upon values for other traits, although formal optimisation would be very challenging. Anyway, a differentiated "portfolio" should guarantee some protection against worst-case outcomes.

Genetic fingerprinting has been developed for quality control to avoid loss of genetic gain through misidentification, and is a prospective tool for averting the need for laborious controlled pollination without sacrificing potential genetic gain.

Progress has continued in development and adoption of clonal forestry, but its fully satisfactory implementation still poses challenges. However, major technical progress has been made in cryopreservation to control maturation state, with much better "genotype capture" to avoid amenability to cryopreservation becoming an important selection criterion. It allows clones to be conserved for future revival while they are screened for the breeding-goal traits. Nevertheless, the goal of being able to rejuvenate any clone, whatever the maturation state, remains elusive.

Radiata remains the context for developing new software-based technologies associated with modern plantation forestry, for modelling growth and product out-turns as decision- and planning aids, for using remote sensing for crop inventory, and for precision control of machinery in the field and in wood processing.

Progress has also continued on developing genetic transformation as a genetic-engineering (GE) technology for genetic improvement. A pilot success has been achieved in genetic transformation of radiata to produce syringyl lignin instead of guaiacyl lignin, which would make chemical pulping easier and cheaper. However, compatibility of this change with field fitness is quite unproven. Moreover, any quest to apply GE faces very elaborate and expensive regulatory protocols in New Zealand and Australia.

Also, DNA markers are being vigorously explored as a tool for earlier and more cost-effective genetic selection. This poses major challenges because of the essentially wild state of the genetic system, a huge genome, an apparent paucity of individual genes of large effect, and the delays and difficulties in obtaining good field-performance information for detecting and verifying informative genomic regions. Disease resistance, however, appears a promising avenue for such genomic selection.

Fresh biotic alarms have occurred in recent years, mainly involving diseases caused by *Phytopthora* spp. They continued a pattern involving pathogens with no prior record of being significant. These alarms have prompted fresh research on breeding for disease resistance, including a search for cross resistance that would confer simultaneous protection against multiple pathogens.

Since the mid-1990s tensions have continued between those charged with advancing breeding programmes along classical lines and those researching new DNA technology for genetic improvement. Allocating resources between the two camps remains a fraught issue. The latter have made big advances, but "killer applications" remain elusive.

While the domestication of radiata has come a long way, it has much further to go, as we explain in the final chapter.

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