

Achievements in forest tree genetic improvement in Australia and New Zealand

10: *Pinus radiata* in New Zealand

R.D. Burdon^{1,2}, M.J. Carson³ and C.J.A. Shelbourne⁴

¹Scion (New Zealand Forest Research Institute Ltd), Private Bag 3020, Rotorua 3046, New Zealand

²Email: rowland.burdon@scionresearch.com

³Forest Genetics Ltd, PO Box 35, Ngongotaha, Rotorua 3041, New Zealand

⁴99 Acacia Road, Lake Okareka, RD 5, Rotorua 3076, New Zealand

Revised manuscript received 24 October 2008

Summary

Pinus radiata is the subject of much the largest and longest-running tree breeding program in New Zealand. Very intensive plus-tree selection began in the early 1950s, the first seed orchard planting was in 1958, and the first orchard seed was collected in 1968. By 1985 seed orchards could meet the national planting needs, which helped prompt an innovative seed certification scheme.

Selection began in local, 'land-race' stands. That proved appropriate, but better knowledge led to research on material from the species' entire natural range and then to further seed importations from natural stands, mainly for future genetic resources.

Initial plus-tree selection largely addressed poor tree form in the central North Island. This led to selecting a 'short-internode' ('multinodal') branching ideotype, with great improvements in general tree form and substantial gains in growth rate. A distinctive portfolio of several breeds, representing different breeding goals, has since been developed for the diverse planting sites and the various end products. By contrast, the original regionalisation of seed orchards proved largely unjustified. Despite early research indicating good heritabilities, wood properties have figured significantly in breeding goals only since growers substantially reduced harvest ages, but they are now intensively researched.

The breeding program was greatly expanded from 1968 to meet the needs of multi-generation breeding. This was one of the program's contributions to developing breeding strategy as a discipline, various of which were reflected in the 1986 Development Plan. Industry uptake of tree breeding has since posed challenges in maintaining genetic variability for a secure, long-term underpinning of the program.

Special genetic-gain trials were first planted in 1978, to demonstrate and quantify genetic improvement, and to help update forest out-turn predictions. The gains achieved in tree form helped induce New South Wales State to affiliate with the New Zealand program, following significant earlier contributions of breeding material to Australian breeding programs.

Improved technologies for seed orchards and vegetative propagation have facilitated development of the breed portfolio

and more specific customisation of seedlots. Becoming able to deliver genetic gain through controlled pollination has allowed changes in the structure of the breeding population. Further changes are resulting from an increasing capability to reconstruct pedigrees after open pollination. Developments towards full clonal forestry have faced obstacles, but offer greater genetic gains and a more precise customisation, and clonal forestry is now being vigorously commercialised.

Having a single, large Forest Service until 1987 undoubtedly favoured the development of a very strong tree improvement program. Since then, continuing institutional changes, which are reviewed, have posed numerous challenges.

Keywords: tree breeding; breeding programs; history; planning; seed orchards; vegetative propagation; genetic improvement; traits; *Pinus radiata*; New Zealand

Introduction

The early introduction of *Pinus radiata* D.Don to New Zealand (Shepherd 1990; Burdon 2001) is similar to and appreciably intertwined with the its introduction into Australia (Wu *et al.* 2007). From 1859 into the mid-1860s importations were made basically on a specimen-tree scale, from Britain or via Australia. The species thrived so well that by the late 1860s larger-scale importations had begun from California, and are known to have continued until 1882, by when New Zealand plantings could evidently meet the considerable demand for seed.

Pilot-scale plantations were established from the late 1860s, and even before 1914 there were enthusiastic promoters of the species. Only after 1921, however, was there a massive commitment to *P. radiata* as a forest plantation crop, and by around 1935 it represented nearly three-quarters of the plantation estate. After *Dothistroma* needle blight appeared in the 1960s and affected the other main pine species even more, this proportion rose to and remained at around 90%. Largely because of this pre-eminence, *P. radiata* is the subject of much the largest and longest-running forest tree breeding program in New Zealand.

Plantations of *P. radiata* now occupy 1.6 million ha. The species is the basis of major export industries, with a total annual roundwood

harvest of nearly 20 million m³. The contribution of the forestry sector (MAF 2007) including derived industries, which is around 95% based on *P. radiata*, is estimated at about 3.5% of the GDP (over US\$2.5 billion annually), and 10% of the country's total export receipts, based on 7% of the land area. This is despite the present depressed state of the sector, certain corporates having focused on producing commodity products and on log exports, and some correction of over-harvesting factors that obscure the species' full contribution to wealth. In addition to producing wood *P. radiata* makes important contributions to soil conservation and provision of farm shelter, the shelter plantings containing an additional timber resource.

Pinus radiata became the strongly preferred species for commercial planting because of its rapid growth, ease of establishment and ability to thrive on a wide range of sites, despite its very limited record as a timber. Nevertheless, it was in glaring need of genetic improvement. While its tree form often left much to be desired, the nature of tree-to-tree differences in form and branch habit, and in health and vigour, strongly suggested much genetic variation. This presumption was strongly supported by results (Fielding 1953) from pioneering work in Australia that began in the 1930s.

With experience from other tree species, and the available evidence for genetic variation in *P. radiata*, a commitment was made to intensive breeding in the early 1950s. Some enthusiasts had already been identifying outstanding phenotypes, but effort was now concentrated at the Forest Research Institute (FRI) at Rotorua within the New Zealand Forest Service. Very intensive plus-tree selection was done, largely aimed at addressing the problems of tree form, in stands on the volcanic plateau of the central North Island, where a high proportion of the *P. radiata* plantings were located. Delivery of genetic improvement was pursued through clonal seed orchards in which plus-tree grafts were planted together to pollinate each other.

Various of the technical advances in breeding were reviewed by Shelbourne *et al.* (1989). The achievements in the program are of great significance, not only in their local impact, but also in their seminal influence on the technology, quantitative methodology and strategy of breeding programs overseas and with other species in New Zealand.

The size and complexity of the breeding program mean that the story is also complex. Accordingly, the emphasis in this account is on tracing various threads in time, with some overlap in coverage, rather than attempting a purely chronological account. While ostensibly technical, the story cannot be considered in isolation from institutional factors. Inevitably, this account reflects in some degree personal viewpoints.

A summary of the various series of clones selected as prospective parents is given in Table 1 (updated from Jayawickrama *et al.* 1997b). Giving the particulars of the series, and indicating generation-to-generation lineages, it serves as an historical backdrop for this account.

Initial breeding operations

Operational breeding of *P. radiata* began in earnest soon after the appointment in 1951 of Ib Thulin. A pupil of the Danish tree

breeding visionary C. Syrach Larsen, Thulin was energetic and forceful, and enjoyed the full support of the then Director (later Director-General) of Forestry, A.R. Entrican. Some enthusiasts had earlier identified outstanding individual phenotypes, but Thulin led systematic and very intensive plus-tree selection (about one tree per 100 ha), mainly during 1953–1958 in stands planted during the 1925–1935 planting boom, to produce the '850', '668' and '767' clonal series (Table 1). This was done with limited research (almost all in Australia) to back up the strong visual impressions of great genetic variability in *P. radiata*.

Very detailed records were kept on individual plus trees, including determinations on a number of wood properties, but little use was actually made of the wood data. Open-pollinated seed was collected, and the clones archived in clone banks, for controlled crossing and for producing grafts for seed orchards. By 1966, however, only about 30 parents had really been progeny tested, as open-pollinated progenies.

Biogeographical background

When the breeding program began, *P. radiata* was thought to come only from three nearby localities on the coast of mainland California, and that therefore provenance variation would be unimportant, in contrast to the situation with several other exotic species. In this belief, with the availability of very extensive local stands, selection in local, land-race stands was logical. However, the three Californian mainland populations were discrete, and early work in Australia showed that they differed in some characteristics (Fielding 1961a). Moreover, two populations of pines on Guadalupe and Cedros Islands (belonging to Mexico) were also confirmed as belonging to the species (Fielding 1961b; Axelrod 1980; Bannister and McDonald 1983), further indicating that there was geographic diversity within the species and that therefore provenance variation could be of interest for some traits of economic importance.

Serious study of the quantitative genetic architecture of the species was launched in the mid-1960s, with planting of a large provenance–progeny trial on two sites in Kaingaroa Forest (Burdon 1992; Burdon *et al.* 1992a,b,c) and with small, step-out trials in three other parts of the country (Shelbourne *et al.* 1979). These trials confirmed substantial differences among provenances in averages for growth, disease resistance, some site tolerances and some wood properties. All populations, however, showed similar patterns and levels of tree-to-tree genetic variation (Burdon 1992), but tended to be inferior to local, land-race stocks for health, growth and form.

The results prompted a major follow-up collection in 1978 of seed from the native stands on the Californian mainland, organised jointly by CSIRO, Australia, and FRI, led by Ken Eldridge (CSIRO) and Tony Firth (FRI) (Eldridge 1978). From New Zealand's share of the seed a country-wide network of provenance trials was established, plus substantial gene-resource plantings. Overall, a picture has emerged of the comparative site tolerances of the different native populations (Burdon 1992; Burdon *et al.* 1997b), which can be supplemented by results from the Australian plantings from that seed collection (e.g. Johnson *et al.* 1997).

Differences among the provenances evidently reflect a combination of both genecological adaptation and important

Table 1. List and particulars of clonal series of plus-tree and advanced-generation selections (adapted and updated from Jayawickrama *et al.* 1997b). Some very minor categories, imported select material, and some series that were abandoned early, are omitted. Numbers of selections may or may not include clones that were not successfully propagated and or represented in progeny trials. Series listed in boldface have so far been important providers of later generations of selections.

Date selected	Series code	No. selected	Selection criteria (in addition to health and vigour and straightness)	Remarks (location of ortets and other particulars)	Age (y)	Generation
1950s	850	140	Straightness; light, wide-angled branching; no low stem cones	Mainly central North Island, and 'multinodal'. Relatively few used in seed orchards or for further breeding	Mostly ca 30	1
1950s	668	51	Straightness; light, wide-angled branching; no low stem cones	Canterbury. Mainly breeding dead end	Mostly ca 30	1
1950s	767	19	Straightness; light, wide-angled branching; no low stem cones	Southland. Mainly dead end	Mostly ca 30	1
1966	266	362	General form and above-average wood density	Kaingaroo, propagated as clones. Breeding dead end	5–7	1
1967	867	66	Dothistroma resistance	Pumicelands (volcanic plateau)	ca 8	1
1968	268	588	Short-internode (multinodal) habit	Kaingaroo	12–18	1
1969	869	30	Dothistroma resistance	Imports from Kenya	ca 8?	1
1970	870	97	Diplodia resistance	Tarawera Forest. Dead end	3–7	1
1970	870	104	Long-internode habit	Kaingaroo	12–18	1
1973	873	35	Long-internode habit	Including some 850 control-pollinated (CP) offspring	5	1–2
1973	873	120	Multinodal	850 CP offspring (very young), cloned and tested	5	2
1974	874	162	Frost resistance	Abandoned	4	1
1975	875	100	Multinodal, above-average corewood density; (early flowering)	Open-pollinated (OP) 268 offspring	5	1.5*
1980	880	188	Multinodal; needle retention	OP 268 offspring	10	1.5*
1983	883	100	Long-internode, needle retention	OP 870 offspring	12	1.5*
1985	885	468	Basic criteria, but getting mostly multinodal	Land race, pumicelands	17–22	1
1986	886	120	Basic criteria, but getting mostly multinodal	Native populations, ex situ, largely Guadalupe	ca 20	1
1986	886	652	Early vigour	Mainly CP 268, 875 and 870 offspring, archived as cuttings	1	2–2.5 [§]
1986	286	17	Basic criteria	Californian mainland, ex situ	ca 20	1
1987	887	243	Basic criteria, but getting mostly multinodal	Mainly as for 885, some international	ca 20	1
1988	888	283	Basic criteria, but getting mostly multinodal	Land races, various regions	Varied	1
1988	188	30	Basic criteria, but getting mostly multinodal	CP 850 offspring	ca 15	2.5 [§]
1988	288	44	Basic criteria, but getting mostly multinodal	CP 268, 975 and 880 offspring	6–7	2–2.5 [§]
1989	889	550	Early vigour and form	CP 268 offspring, archived as cuttings	4	2–2.5 [§]
1989	889	23	Basic criteria	Guadalupe, ex situ	8	1
1992	892	80	Basic criteria, but getting mostly multinodal	CP 850 offspring	7	2–2.5 [§]
1994	894	128	Basic criteria plus needle retention	Californian mainland ex-situ plantings	24	1
1999	899	25	Long-internode	CP 870, 873 and 883 offspring	ca 10	2.5–3 [§]
2000	–	10	Long-internode	CP 870 offspring	10	2.5 [§]
2003	–	113	Basic criteria plus wood stiffness and straight grain	CP offspring, mainly of 268, 875 and 880	ca 10	2.5–3 [§]
2004	–	73	Basic criteria plus wood stiffness and appearance	CP offspring, mainly of 268, 875 and 880	ca 10	2.5–3 [§]
2006	–	64	Basic criteria plus wood stiffness and appearance	Forwards selections in OP 888 offspring	17	1.5 [§]

*Half generation deducted for non-select nature of pollen parents

[§]Half generation added for use of parents chosen on basis of progeny-test information

founder effects (Burdon 1992; Millar 1999). The latter doubtless arise from a complex history of isolated populations subject to colonisations, coalescences and local extirpations which would have been driven by climatic changes and sea-level changes from the Pliocene era onwards. Overall, the northernmost native populations, from Año Nuevo and Monterey, from which our local stocks appear to have been entirely descended (Burdon 1992; Burdon *et al.* 1997a), proved to be the best adapted overall to New Zealand conditions. Even so, they have shown different adaptive profiles, Año Nuevo doing better in the far south, and Monterey better in the far north, especially on phosphorus-deficient clays. Some New Zealand material has shown marked adaptive shifts even without intensive artificial selection (Burdon 1992; Burdon *et al.* 1997b). Monterey is considerably under-represented in land-race ancestry, in relation to the comparative sizes of the two populations. Despite the general superiority of the two northernmost provenances all provenances have features of interest, so it seems prudent to maintain and selectively exploit the species' full geographic diversity. Indeed, a pedigreed Guadalupe Island breeding population is being maintained (Low and Smith 1997), and pilot-scale commercial plantings of F1 hybrids with New Zealand land-race material have been made.

Research activities

Research and operational breeding began largely in isolation from each other. While the operational breeding was headed by Thulin, basic research on the variation and genetics of the species was pursued by Martin Bannister, a protégé of Lindsay Poole, Entrican's Deputy. Poole had headed the Botany Division of the Department of Scientific and Industrial Research (DSIR) and arranged the transfer of Bannister to FRI, where he perceived a need and opportunities for the basic research.

Even within the applied breeding program, some experimental crossing was done with a clone that was homozygous for a recessive gene causing a fastigate habit and some other anomalies. Studies of resulting self-pollination were also done, showing very variable effective self-fertility and levels of inbreeding depression among the viable seedlings (Wilcox 1983; Kumar 2004a). Some early controlled crosses among seed-orchard clones, planted in 1958, showed striking genetic improvement.

In fact, recording the results from the operational breeding entailed much research — in planning the breeding strategy, devising mating and field designs, analysing and interpreting data from progeny-trial assessments, and evaluating genetic gain. The consequent research information included early estimates of genetic parameters, viz. variances, heritabilities and genetic correlations between traits, albeit involving select material rather than base populations. Conversely, much information, and subsequent impacts on the breeding operation, was eventually to come from the effort on basic research. Some of that basic research information included confirming that genetic parameter estimates obtained from select material did not differ greatly from estimates obtained from base populations (Burdon 1992). Exceptions would involve traits that are both quite highly heritable and have been subjected to strong selection, such as branch cluster frequency.

While not strictly research, the use of index selection by Mike Wilcox in the early 1970s was notable for being among its first

applications in forestry. Also, it gave a platform for making in-house refinements of selection methodology.

As the breeding program advanced theoretical work proceeded, and included predicting genetic gains from alternative selection scenarios (Shelbourne 1969); comparing expectations of gains from alternative mating designs (van Buijtenen and Burdon 1990); developments in producing an integrated breeding strategy (e.g. Shelbourne 1969; Burdon *et al.* 1978; Shelbourne *et al.* 1986; Jayawickrama and Carson 2000); developing methodology for studying and living with genotype \times environment interaction (Burdon 1977; Johnson and Burdon 1990; S. Carson 1991); developing some variations of index selection (e.g. Burdon 1979); and exploring early-selection methodology (e.g. Franich *et al.* 1986; King and Burdon 1991). The progeny trials were generally very large and well-replicated, so there was little early call for more sophisticated selection methodology that could accommodate unequal information (e.g. widely different amounts of progeny-test data) about different selection candidates.

Regarding field-trial designs, single-tree plots, in various forms, became widely used for both research and operational breeding. The logistics of establishing such trials became much refined, largely through the efforts of Gerry Vincent.

Potential benefits from separate development of a long-internode breed were explored (Shelbourne 1970; M. Carson 1988). Also screening options and field trials were evaluated for development of a *Dothistroma*-resistant breed (S. Carson and Carson 1986, 1989).

Seed-orchard research was soon recognised as a priority, and came to be led by Geoff Sweet. Issues included delayed graft incompatibility, limited conelet production, conelet abortion and external pollen contamination. Solutions identified included better site selection for early and heavy orchard flowering, applying gibberellins to boost flower production, and the institution of crown management methods based on 'meadow orchards' (M. Carson *et al.* 1992). Tony Firth refined controlled-pollination methods, and Mike Carson (1986a) demonstrated the potential value of large-scale controlled pollination in a simulation study.

Performance and silviculture of improved breeds has been researched to demonstrate genetic gains, incorporating the gains into growth models for yield predictions (S. Carson *et al.* 1999a), and matching tending regimes to the properties of improved breeds (e.g. M. Carson and Inglis 1989; M. Carson *et al.* 1991). Additional research addressed the profitability of deploying improved breeds (M. Carson 1988), and appropriate deployment to maximise selection gains (M. Carson 1989; S. Carson 1996; S. Carson *et al.* 1999b).

Much research was done on vegetative propagation (Menzies *et al.* 1988; Miller 1991) as a tool to serve controlled crossing, seed-orchard establishment, direct mass-production of planting stock, and research on inheritance of traits. An important end-point was to be true clonal forestry with clones of first choice (see later).

Inheritance of wood properties, mainly density, was investigated before 1970 (see Shelbourne 1997 for references) without impacting much on actual breeding. Much later there came a major focus on wood properties (Shelbourne *et al.* 1997; Sorensson

et al. 1997; Beauregard *et al.* 1999; Kumar 2004b; Dungey *et al.* 2006; Ivković *et al.* 2006; Kumar *et al.* 2006, 2008), going beyond wood density to traits involving solid-wood stiffness and dimensional stability and, potentially, better pulping properties. Much work has proceeded on inheritance of such properties and on developing cost-efficient methods of screening selection candidates. Research into the inheritance of fibre and pulping properties has proceeded (e.g. Uprichard *et al.* 1994; Donaldson *et al.* 1995; Shelbourne *et al.* 1996; Kibblewhite and Shelbourne 1997; Evans *et al.* 1999), but application is subordinate to meeting needs for solid-wood products.

For managing breeding populations, the program has made some use of Dag Lindgren's measure of effective population size, namely status number (Gea *et al.* 1997).

Use of isozymes for research on the species was very limited because work was done in Australia and USA while their value for New Zealand's purposes was not seen as great. Use of DNA technology is now being vigorously pursued, beginning in the early 1990s with emphases led by Sue Carson on fingerprinting and marker-aided selection (M. Carson *et al.* 1996). Applications for genetic fingerprinting, verifying both clonal identity and parentage, are now routine. Genomic studies are being pursued as an aid to selection, population management (Burdon and Wilcox 2007), and targeting new attributes. Genetic transformation is being used both as a research tool and for developing a capability for operational use (Walter *et al.* 1998).

Analyses of both the benefits and risks associated with clonal forestry have been carried out (Burdon 1986; M. Carson 1986b; M. Carson and Burdon 1991; Aimers-Halliday and Burdon 2003; Burdon and Aimers-Halliday 2003; Kube and Carson 2004) including possible use of genetic transformation (Walter *et al.* 1998; Burdon and Walter 2004).

Breeding achievements

Controlled crossing

Controlled crossing was practised soon after the early plus-tree selection in the 1950s. However, this had little direct impact on the long-term development of the program. The main initial crossing effort employed the North Carolina II (NC II, four-tester) mating design, a misguided borrowing from chicken breeding (which had quite different reproductive constraints). Much of the resulting seed was destroyed by a coolstore malfunction in 1967, which was to some degree a blessing in disguise. However, this controlled-crossing phase did produce plantings that strikingly demonstrated the genetic gains that could be achieved by intensive selection of parents and controlled pollination.

For managing the breeding population, within which cumulative genetic gain is achieved over generations, controlled crossing was until recently seen as a key feature. Research on achieving large-scale controlled crossing using pollination techniques that avoided the need for bagging the conelets never produced an operational solution. In the event, open-pollinated progeny trials proved the principal means of generating large breeding populations, as well as testing the seed parents. In the last few years, however, marker technology has developed to the point where it promises to allow pedigree reconstruction that may largely obviate the need

for controlled pollination for producing advanced generations of the breeding population (Kumar *et al.* 2007a,b).

Seed orchard development and performance

Getting the seed orchards into full production entailed a long, steep learning curve. Although the species could be very easily grafted, delayed graft incompatibility was a problem, very often striking just as the grafts were approaching commercial levels of seed production (Shelbourne *et al.* 1986). Siting of the first orchards was dominated by seeking pollen isolation from unimproved *P. radiata*, which led to choice of unsuitable sites without actually achieving good isolation. Early pollen production (in the first 6–7 y) within orchards was minimal, and was evidently almost completely swamped by pollen blown in from massifs of distant stands (C.J.A. Shelbourne unpubl.). Later, as the orchards were enlarged and the grafts came into full pollen production, 'internal' isolation became more effective. With sub-optimal siting, however, losses by conelet abortion were a big problem (Sweet and Thulin 1969) until the ramets grew above the frosty, ground-level microclimate.

As an interim measure, until seed orchards came into full production, select-tree seed collection (about 25 ha⁻¹) was done in unimproved stands. Initially it was 'felling select' after pre-harvest felling of 'old-crop' stands (generally 30–40 y old). Later it was 'climbing select', on much younger stands (generally age 12–20 y). This gave modest genetic improvement in form and growth rate, but much less than from the seed orchards established using intensive plus-tree selection.

Despite their early woes, the open-pollinated seed orchards did work. The first collection of orchard seed was made in 1968, ten years after the first orchard planting. And by 1985, orchards were producing enough seed to meet the country's needs (Shelbourne *et al.* 1986). Indeed, they were soon able to cater for substantial overseas demand, especially from Australia. But, while the classical orchards were coming into full production, alternative orchard systems were being vigorously researched. The importance of siting became very clear, thanks largely to the success of a high-quality orchard site at Amberley, near Christchurch. A good site allowed seed production near ground level, opening up the prospect of achieving better control of pollination, while producing the seed at a convenient height — much as in classical apple orchards. Importantly, Amberley became the first successful control-pollinated orchard with the species.

Pinus radiata often appears to produce abundant seed, because one sees cumulative crops of persistent cones, but it is not actually a profuse seed producer. Various attempts were made to stimulate greater flowering. Early on, they included bark ringing, and successful but undocumented grafting on to a surprising range of pine species, while achieving little if any stimulation. Much more successful was the subsequent use of gibberellin injection (Ross *et al.* 1984), which is now routinely used in commercial orchards. However, the biggest factor was choice of site, flowering and seed production being abundant on sunny, low-rainfall sites close to the sea (Dickson 1996). This realisation overtook much painstaking seed-orchard research. Although such sites tend to be highly priced owing to demand for premium vineyard land, breeding archives and seed orchards are now routinely established on them,

Table 2. Percentage improvement of mean age-12 stem diameter performance for seedlots of different Improvement Ratings (GF values) at a selection of sites (from C.T. Sorensson and C.J.A. Shelbourne, unpublished), relative to performance of GF2. Differences among seedlots were statistically significant ($P < 0.001$) overall and at most individual sites. Values for the six large-plot trials averaged slightly higher than for the remaining, small-plot trials.

GF value	Site*														Mean
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	
8	-4	2	6	6	1	4	4	3	0	0	-2	5	6	5	2.6
10	0	4	6	4	4	4	1	3	2	5	5	8	2	4	4.5
14	2	12	18	4	8	6	15	6	9	17	12	6	12	4	9.4
16	9	10	12	9	9	9	16	11	12	16	9	9	11	17	11.1
22	4	16	20	15	15	16	12	19	19	24	19	10	18	25	16.6

*Spread throughout New Zealand

owing to their much greater capacity for producing early and increased seed yields. With seed production possible near ground level, large-scale controlled pollination became feasible, thanks to new methods and technologies being developed (M. Carson *et al.* 1992). This development has largely blurred the original demarcation between seed orchards and crossing archives. The feasibility of using nursery cuttings (which can be supplemented by tissue culture) to mass-produce planting stock from scarce seedlots of the highest available genetic merit represented a further departure from past practices (Menzies *et al.* 1992).

There is a current thrust on testing top-grafting orchard technology from southern USA to assist early seed production.

Nature and level of genetic gains

The original plus-tree selection gave dramatic improvements in tree form and considerable improvement in growth rate, despite wide variation among plus trees in their resulting breeding values. The improvement in tree form was evident as greatly reduced malformation, much better straightness, and lighter, wide-angled branching (e.g. Shelbourne *et al.* 1986; M. Carson 1989; S. Carson *et al.* 1999b). The branching pattern, however, was quite strongly 'multinodal', or short-internode, reflecting the habit of the trees that met the original selection criteria. Early gains achieved from the open-pollinated orchards, however, were diluted by half (Shelbourne unpubl.), reflecting the apparently almost 100% external pollen contamination.

While control seedlots were routinely included in progeny trials, a need emerged to both establish systematic benchmarking of genetic advance and get a measure of realised genetic gain at the crop rather than at the individual-tree level. That led to the establishment of specialised genetic-gain trials, of which the first were planted in 1978. Two complementary types of trial were used:

- row-plot, using more seedlots and planted on more sites, which were designed to give cost-efficient ranking of seedlots, albeit in the comparatively short term
- large-plot, square, 10 × 10 trees, using fewer seedlots on fewer sites, designed to compare seedlots for whole-crop performance, on a longer time frame. Some variations of silvicultural regime were also incorporated. Such trials were eventually used to compare growth-model parameters between seedlots representing different breeding goals and levels of improvement.

Some genetic gains for stem diameter (dbh) observed in genetic-gain trials, in relation to different Improvement Ratings (see the section on the seed certification scheme), are shown in Table 2. The pattern was remarkably consistent among sites. The large genetic gains could also be conveniently expressed in terms of percentage acceptable stems for pruning, and growth rate. Comparisons between select and control material for percentage acceptability can be very site-dependent, but can be dramatic when the overall mean is in mid-range. However, relative dbh performance of improved New Zealand seedlots was less consistent across sites in Australia (Low *et al.* 2006).

Comparisons involving growth rate face the difficulty of projecting what are early-in-the-rotation individual-tree growth data (typically at around one-third harvest age) into whole-crop, harvest-age yields. This has been addressed by S. Carson *et al.* (1999b) who used data from genetic-gain trials to construct growth models for seedlots representing different levels of genetic improvement (termed 'genetic gain multipliers'). Interestingly, genetic gain was expressed much more strongly in the basal-area growth function than in height growth, in contrast to a pattern of genetic gain mimicking an increase in site index. While the projected percentage volume gain fell with crop age, it did not do so dramatically (Table 3). Compared with a climbing select seedlot (rated GF7 — see later for explanation) the projected volume-per-hectare gains at age 30 y were 12% and 19% for an early seed-orchard lot (rated GF12) and a mid-80s standard controlled cross (rated GF22) respectively (although some of these gains may be accompanied by a correlated drop in wood density). Even larger gains have since been reported (S. Carson *et al.* 1999b). Importantly, the reported stem-volume gains came with major gains in standard of tree form. Such genetic gains for stem volume production are evidently greater in absolute terms but less in relative terms on high-quality sites (S. Carson *et al.*

Table 3. Observed and projected percentage gains in stand stem volume production in two improved seedlots (GF14 and GF22) relative to climbing select (GF7) (from S. Carson *et al.* 1999a)

Improvement rating	Age (y)			
	15	20	25	30
GF14	17	15	14	13
GF22	28	26	24	22

1999b). Comparisons among commercial stands have revealed less clear differences (Turner 1997a,b), but those comparisons also lack experimental rigour. Since these genetic-gain trials were established, substantially superior material has been deployed in plantations.

Much of the selection and testing was carried out on pumiceland sites, which have relatively fertile forest soils and receive considerable summer rainfall. This has probably contributed significantly to the gains achieved, since such sites give good resolution of genetic differences for a wide variety of traits.

Impacts of the gains

The direct impacts of breeding come at harvest, long after the breeding has been done. Some indirect impacts, however, come much sooner. With genetically improved stock available, it proved possible to drastically reduce the number of trees planted (Wilcox and Carson 1989), owing to both there being fewer malformed stems and other improvements in tree form. For instance, initial stockings required to ensure enough good, final-crop stems could often be reduced from 1500 or more stems ha⁻¹ (sph) to 600 or even less, with flow-on savings in tending costs. However, initial stockings of under 1000 sph, particularly if final crop stockings are correspondingly low, can lead to reduced control of branch sizes, reductions in wood stiffness, and (at very low stockings) losses in mean annual increment.

Importantly, genetic gain tends to become obvious only several years after planting (S. Carson *et al.* 1999b). Control of size and quality of nursery stock, and thence early survival and growth potential, is seen as being in the hands of the nurseryman.

The improvements in tree form and growth rate were demonstrated by both visual impact and rigorous statistical comparisons of improved versus non-improved plantings. But far more importantly, the gains were so striking that industry uptake of genetic improvement has been almost total. That has created a potential risk factor for forest owners maintaining the broad genetic diversity that might be needed for the long term or in the event of a biotic crisis. Under current levels of diversity, however, this risk should be small, although disciplined and resolute genetic

management will be needed to contain the risk. How rapidly a population base can be eroded by emphasis on among-family selection is illustrated by a calculated status number (Gea *et al.* 1997) of around 60 as at 2005 for the breeding-population component based on the combined '850' and '268' clonal series (P. Jefferson unpubl.) (cf. numbers of selections listed in Table 1).

The seed certification scheme

The seed certification scheme, which includes a rating system based on the levels of genetic gain in seedlots (or planting stock), has played a very large part in industry uptake of genetic improvement. It was prompted by several factors, achieving self-sufficiency for orchard seed in 1985 (Shelbourne *et al.* 1986), the pending commercialisation of tree improvement, and the fact that levels of genetic gain could be expected to continue to rise steadily. The scheme was based on a specific descriptor of genetic merit for each seedlot, namely the Improvement Rating (Vincent 1987). For seed-orchard seedlots representing the mainstream Growth and Form breed a single GF Improvement Rating would be assigned. For a seedlot of a specialised breed, an Improvement Rating would also be assigned with respect to the specialist feature of the breed. Examples of Improvement Ratings for different types of seedlot are shown in Table 4. These ratings are based on performance of individual parents in progeny tests, and cover a combination of growth rate, tree-form, wood quality and disease resistance traits. The ratings were not intended to predict absolute levels of improvement; rather, a higher rating would be an assurance of greater genetic improvement.

Assignment of Improvement Ratings on a 'New Zealand-wide' basis has been facilitated by the generally modest level of rank-change genotype-site interaction (S. Carson 1991; S. Carson *et al.* 1999b), the big exception being considerable interaction for growth between phosphate-retentive clay sites and sites elsewhere in the country (Johnson and Burdon 1990; cf. Matheson and Raymond 1984 and Johnson 1992; Burdon *et al.* 1997b).

The certification process represents an official assignment of a seedlot number, of which the Improvement Rating is the central

Table 4. Improvement Ratings, for Growth and Form (GF), given to different categories of seedlot. Figures are given for 'leading-edge' seedlots, with proviso that they were based on multiple parents. From Vincent and Dunstan (1989) and Vincent and C.B. Low (unpublished).

Category	Years	GF rating
Native-population collection	–	0
Unimproved 'bulk' New Zealand collection	To ca 1962	(1–2)
Felling select	ca 1962–	<7?
Climbing select	1968–	7
850 seed orchard (rogued/reselected, all remaining clones)	ca 1985	14*
268 seed orchard (rogued/reselected, all remaining clones)	ca 1985	15*
268 seed orchard — rogued, top 16 seed parents	1985	19*
268 seed orchard (rogued/reselected, all remaining clones)	1988	16
Top controlled crosses (for vegetative multiplication)	1988	22
Top controlled crosses (for vegetative multiplication)	1989	25
Top controlled crosses (for vegetative multiplication)	1991	26–28
Top controlled crosses (for vegetative multiplication)	1995	30

*Retrospective certification for rating of seed-orchard seedlots after certification scheme came into effect in 1987.

feature, on the basis of information on the composition of the seedlot and on the performance of its components. The secretariat for this is held at Scion, although the further development and support of the system depends largely on the Radiata Pine Breeding Consortium (see later). The scheme has been extremely successful, demand and prices for seedlots being strongly driven by the ratings. Certification is applied to both seed and vegetatively propagated stock as well as to seedlots and seedlings.

In 1998 the seed certification scheme was modified and branded as *GFPlus*, a registered trade mark. More recently, a focus on explicit estimation of breeding values for individual parents based on BLUP (best linear unbiased prediction) has assisted more rapid and frequent estimations of breeding values underpinning the *GFPlus* ratings.

Breeding goals and breed differentiation

Initial plus-tree selection was largely directed at the problems of tree form that beset the very large areas of plantation on the North Island's volcanic plateau, but there was also a significant move to capture expected variation among regional land races (M. Carson 1997). The following criteria were stringently applied: general health and dominant to super-dominant crown status, and freedom from stem malformation, as preconditions; greatly superior stem straightness; regular, light, wide-angled branching; and freedom from cones low on the stem. The last criterion related to the then widespread use of weatherboards for housing, and later fell into disuse. As mentioned earlier, the prescribed branching characteristics entailed, in that region, selecting strongly polycyclic ('multinodal') trees.

In the mid-1950s, separate selection programs were mounted for orchards to serve the Canterbury and Southland regions of the South Island. Selection on those sites produced much less of a shift towards a 'multinodal' branch habit. These selections subsequently performed poorly, however, and this pattern of regionalisation proved to be unwarranted in that genotype \times site interactions between the volcanic plateau and these South Island regions were minor (e.g. Table 2).

When further plus-tree selection began in 1968 the approach to selecting for branching behaviour changed. Greater frequency of branch clusters (or shorter 'internodes') became a selection criterion in its own right, since it was by then known to be both highly heritable and favourably correlated genetically with growth rate, branch size and angle, stem straightness and other components of tree form. As such, it was in effect a classic case of indirect selection. However, it also created a dependence on pruning of the butt-log for clearcuttings of any length (Shelbourne 1970; M. Carson 1988). At the time there was no call from industry for selecting for increased wood density, so this was not included as a selection criterion. During the next few years the realisation grew that density was going to fall as the 'old-crop' (1925–1935) plantings would be replaced in the harvest by much younger crops. However, since a genetic trade-off between density and stem diameter growth was becoming evident, the industry sector was initially deterred from requiring selection for higher density.

Despite the insistent call from industry for the short-internode 'ideotype' (Burdon and Thulin 1966), the breeders decided to also provide for industry the option of growing trees that could

provide significant clearcuttings between knot clusters, in order to obtain clearwood without pruning. For this, so-called 'uninodal' (or generally near-uninodal) plus trees were selected in 1970 (Shelbourne *et al.* 1986), despite the difficulties of obtaining good, straight, vigorous phenotypes of this habit. Clones of these plus trees were used to establish both progeny tests and a seed orchard, and a subsequent second generation of breeding offered substantial improvements (Jayawickrama *et al.* 1997b). Industry demand to date, however, has been limited to a few growers. This initiative represented the first move towards a portfolio of 'breeds' differentiated by breeding goals, superseding the abortive regionalisation of seed orchards (S. Carson 1996).

With the advent of needle blight caused by *Dothistroma pini*, some apparently highly resistant phenotypes were selected in badly affected stands, and some apparently resistant material was imported from Kenya. While these selections generally proved to have superior resistance, the absence of good information on their growth and form meant that they were not really immediately useable in seed orchards. Instead, a subset of the main breeding population was selected on the basis of progeny-trial performance to constitute a *Dothistroma*-resistant breed for deployment on sites of high disease hazard (S. Carson and Carson 1986, 1989; Shelbourne *et al.* 1986). Offspring from resistant parents and tested clones are now being deployed to high-hazard sites for the disease.

In 1970, a small selection program was instigated for resistance to shoot dieback associated with *Diplodia pinea* (Desm.) Kickx (Burdon *et al.* 1982). This work lapsed after initial promise following some equivocal progeny-test results, but the need was reduced owing to a cessation of severe outbreaks. Some selection for improved frost resistance, while promising (Menzies *et al.* 1987), was abandoned in a context of improved establishment practice.

In 1975 selections were made of young trees in an open-pollinated progeny trial, including culling candidates with below-average wood density. Almost 100 selections were made (many of them related) and controlled crossing was achieved in situ on the ortets, and progeny trials established successfully. While several of these early selections remain among the top-ranked seed-orchard parents, some became badly affected by *Cyclaneusma*-associated needle cast. A further round of 200 such selections was made in 1980 (Shelbourne *et al.* 1986), with a strong emphasis on foliage retention in addition to improvements in growth and form.

A fresh round of first-generation selection was made in the mid-1980s to produce around 1000 new plus trees, partly to offset a run-down of breeding population size, and partly to tap the genetic resource represented in unimproved land-race stocks that were being fast replaced by seed-orchard stock (Shelbourne *et al.* 1986). In this selection, branch cluster frequency was no longer a selection criterion in its own right, although most of the selections were towards the short-internode end of the scale.

After about 1990, earlier warnings of problems with wood properties were realised (Cown 1992). Selection for growth rate without regard to wood density had led to some selection against wood density. More important, though, were undoubtedly the combined effects of aggressive adoption of the direct sawlog regime and much shorter rotations aimed at reducing growing

costs. Not only did these factors combine to produce a major drop in wood density, but they also meant that microfibril angle, grain spirality and compression wood incidence greatly increased, leading to poor timber stiffness and instability of timber during drying and in service, while internal checking increased defects in appearance grades. As a result, several wood properties are now being vigorously addressed in selection, as well as being researched for various solid-wood uses and pulping properties (see 'Research activities' section, paragraph 11).

Creating a 'portfolio' of breeds (Jayawickrama *et al.* 1997a; Jayawickrama and Carson 2000) has been prompted by a combination of factors. The products and end uses for which *P. radiata* is grown are diverse, both appearance and structural grades being important in its solid-wood markets. Also, the large phenotypic effects of sites where the species is grown mean that divergent breeding goals are indicated for different site types, even without important rank changes among sites due to genotype-site interaction. While the mainstream program became designated the Growth and Form breed, and the 'uninodal' component the Long Internode breed, there was also the *Dothistroma* Resistant breed. Since then, some resistance to *Dothistroma* and *Cyclaneusma* needle casts have become essentially universal selection criteria. Meanwhile, the breed portfolio has morphed into Structural Timber (after a period of High Wood Density) and Clear Cuttings, in addition to Growth and Form. These breeds have been embodied in the breeding program as specialised 'elite' components of the breeding population.

With the available propagation technology it is now possible to customise seedlots and clonal mixes to meet the demands of growers. In retaining differentiated breeds, there is no need to have breeds genetically disconnected from each other (Burdon 1986).

Exploiting the breed portfolio depends strongly on appropriate deployment to site types, but the portfolio can also serve as an instrument to spread market risks.

Where breeding goals involve multiple traits, especially where there are adverse genetic correlations between traits, there is a call to know the comparative economic worth of genetic gain in different traits. However, the complex production system for *P. radiata* in New Zealand, with wood going into diverse processes and end products, makes this task very challenging. The task has been largely finessed by creating the breed portfolio, which implicitly assigns among breeds different sets of economic weights to different traits, but there are areas remaining to be addressed. Apart from the genotypic trade-off between internode length and general growth and form, the trade-off between growth and wood density, and some other wood properties (Wu *et al.* 2008) will continue to pose challenges.

Hybridisation

Pinus radiata can be crossed readily with only two, very closely related species, *P. attenuata* and *P. muricata*. A very small amount of natural hybridisation occurs with *P. attenuata*, reflecting high crossability. Originally pursued for resistance to frost and drought (Gea *et al.* 2006), the hybrids with *P. attenuata* have shown greatly superior resistance to snow damage (Dungey *et al.* in MS). With

P. muricata, only its southern populations, which are of least interest, have proved at all crossable with *P. radiata*.

Of interest are several Mexican–Central American pine species that are weakly or potentially crossable with *P. radiata* (Dungey *et al.* 2004). Being adapted to summer rainfall, they have either known or likely resistance to various diseases that, if they became established in New Zealand, could affect *P. radiata* very badly over big areas where it is now grown. Achieving and exploiting such hybridisation, however, would certainly require much increased commitment.

Evolution of breeding strategy and population management

When the first seed orchards were established the roguing or reconstituting of the orchards on the basis of progeny-test results was seen, at least tacitly, as almost an end-point of breeding. Yet there were two key realisations that tree breeding would involve far more than that. One was that the modern levels of domestication and genetic improvement in traditional crop plants and animals have often taken very many generations of breeding, even though applying a scientific approach was quite recent. The other was that very wide genetic diversity would be needed to assure long-term genetic advance.

In the late 1950s, Martin Bannister, inspired largely by the writings of the Russian, Vavilov, and appreciating that the species included the Guadalupe pines, if not also the Cedros ones, called for incorporating the full range of the species' genetic diversity into the improvement program (Bannister 1959). This was implemented, at the research level, in the Genetic Survey experiment (see Burdon 1992 and other papers in series).

On another front, Tony Shelbourne, from contact with the late Gene Namkoong at North Carolina State University, came to the operational breeding with fresh eyes. He saw that the super-intensive plus-tree selection (which produced the '850' series), combined with both culling clones on their progeny-test performance and use of an inappropriate mating design, was heading for a problem. As breeding moved into later generations, the genetic base was going to narrow rapidly, especially if the NC II four-tester mating design were to be retained. Accordingly, he arranged to broaden the genetic base dramatically. In 1968 around 600 new plus trees were selected, in younger stands (12–18 y) in which some traits were actually expressed better, and accepting less intensive selections (about one tree in 1.2 ha) in order to get the numbers. These plus trees were called the '268' series, from which open-pollinated seed was used to establish three very large progeny trials and some smaller ancillary trials. These trials, while initially aimed at backwards selection of parents for seed orchards, became the core of the breeding population providing forwards selections for further breeding.

The question of mating designs was re-examined after disillusionment with the NC II, focusing on the relative merits of different mating designs. It was eventually concluded that type of mating design was less important than appropriate representation of individual parents, and that individual parents would never need to be involved in large numbers of crosses. Use of complementary designs, to serve different purposes (Burdon and Shelbourne 1971)

was an option. A novel mating design recently attempted was the female tester (Jayawickrama *et al.* 1997b), mainly for testing new selections against a set of four or five standard seed parents. Among other things, this design exploits the species' feature of consistently precocious pollen production. In practice, however, it did not meet expectations, so it has been dropped in favour of simpler designs.

Also, with a stay by Bill Libby in 1971, the overall organisation of genetic material, of which mating designs were only a part, was reviewed. From this crystallised the concept of the hierarchy of populations (Libby 1973) for resolving the conundrum that intensive selection, while needed for achieving high genetic gain, will erode genetic diversity that is likely to be needed for future gains. At the top of the hierarchy, representing the greatest genetic diversity but the narrowest genetic base, is the **production population**, which was seen as consisting of seed orchards (or stoolbeds for mass vegetative propagation). Underpinning that population comes the **breeding population**, representing somewhat less genetic gain but greater genetic diversity, in which cumulative genetic gain is pursued over generations of selection, intermating, selection, and so on. Underpinning that are the **gene resources**, representing the least if any genetic gain but the greatest genetic diversity. Any movement of genetic material between levels was foreseen as being up the hierarchy.

It had become realised that, in breeding strategy and population management, it was easy to find oneself 'painted into a corner', with no quick, easy option for correction. Thus tree breeding strategy became something of a discipline in its own right (e.g. Shelbourne 1969; Burdon and Shelbourne 1971; Burdon *et al.* 1978) which attracted considerable effort within the *P. radiata* breeding program. In developing a breeding strategy, choice of options for individual components came to be seen as being much less important than ensuring the strategy hangs together as a total, failsafe package. Thus a good strategy is seen as a set of measures that are designed to ensure, in conjunction, a near-optimal outcome in the face of the various biological and market uncertainties. This was embodied in the 'Development Plan for Breeding Radiata Pine' (Shelbourne *et al.* 1986), which contained a comprehensive statement of the breeding strategy.

Advances in breeding technology call for modifications in strategy. A major opportunity arose with the prospect of relying solely on controlled pollination for producing commercial stock (M. Carson 1986a), either by mass controlled pollination or by vegetative multiplication of control-cross seed. This was supported by the ability to assure long-term future outcrossing by having the breeding population separated into only two disconnected sublimes (Burdon 1986), rather than having as many sublimes as clones in the orchard. This in turn made sublining a practicable option within the breeding program, which has since been adopted (Jayawickrama and Carson 2000).

The concept of 'nucleus breeding', which had been devised in animal breeding and introduced to forestry by Paul Cotterill of CSIRO, Australia (Cotterill 1989), became incorporated in the breeding strategy. For this there was a platform in the presence of existing or emerging breeds, with a central Growth and Form breed complemented by several overlapping 'special-purpose' breeds for different breeding goals. The breeding population

was subdivided into 'Elite' and 'Main' strata, the Elite stratum representing the several special-purpose breeds. Contentiously, it was recently decided to essentially collapse the differentiated breeds within a single Elite, in combination with a 'rolling front' strategy (Dungey *et al.* in press). It seems likely, though, that various 'sub-Elites' for differing breeding goals will persist within a continually-reconstituted 'main Elite', which allows for the fact that there was never any reason for breeds to be unrelated to each other (Burdon 1986).

Cloning individual offspring within the breeding population has some theoretical advantages for forwards selection in the breeding population, as well as for clonal forestry (Shelbourne *et al.* 2007), especially if there is substantial genotype \times site interaction. It has been pursued on a pilot scale in the Elite stratum (Dungey *et al.* in press), and is under consideration for wider adoption.

It is now also proposed to rely on open pollination for the Main breeding population (Dungey *et al.* in press). This can either occur through maintaining population sizes and diversity at a sufficient level that pedigree information is not required, or it may be possible to maintain pedigree with the potential to reconstruct pedigrees using DNA markers (Kumar *et al.* 2007a,b; Shelbourne *et al.* 2007).

In the longer term, DNA technology may bring many additional changes in population management (M. Carson *et al.* 2004; Burdon and Wilcox 2007).

Propagation technology and clonal forestry

Vegetative propagation has been used in the NZ program in several ways:

- as a breeding tool, securing select material so it can be used for crossing
- for establishing seed orchards, typically by making grafts
- for mass-producing planting stock
- as a research tool, providing quantitative genetic information
- provisionally, for replicating individual offspring in the breeding population (see three paragraphs back).

Grafting and orchard establishment

As mentioned earlier, grafting readily secured clones for archiving, crossing and establishing seed orchards. The problem of delayed incompatibility (Sweet 1973), however, was never fully solved. Rather, it became easier to live with as seed-orchard work shifted to more favourable sites where incompatibility appeared to be less, and would cause less trouble when it did occur. To circumvent severe incompatibility, especially on North Island sites, rooting of cuttings of mature material was successfully developed (van Dorsser and Faulds 1991). It involved ringbarking shoots to be rooted, cutting the main buds off the tips of the shoots, covering the ringbarked zone with foil, and setting the shoots after callus had been induced. Although the procedure was cumbersome and quite expensive, it sufficed for orchard establishment. All recent seed-orchard establishment, however, has been on more favourable sites, and grafting has been used universally for the propagation and establishment.

Mass-production of planting stock

It was long known that *P. radiata* could be grown as rooted cuttings. Indeed, it was done in Britain at least as early as 1839 (Elwes and Henry 1910, p. 1083). The feasibility was rediscovered in both New Zealand and Australia in the 1930s (Field 1934; Jacobs 1939; Fielding 1954). It was also recognised that using clones offered the prospects of both capturing non-additive gene effects that could not be captured in seed production, and avoiding unwanted genetic segregation. As such, it offered greater potential genetic gain, and more uniform raw material for the processor. An additional attraction lay in using cuttings with some maturation ('physiological ageing') to avoid the poor stem form typically associated with the juvenile habit of the species. This approach was pursued in the 1960s (Wilcox and Thulin 1976), but failed, because of the difficulty and expense of collecting cuttings with significant maturation, along with the problems of maintaining clones in rootable state by the time they have been field-tested. Even in material that could still be rooted, maturation tended to reduce growth potential in the resulting plantations (Sweet and Thulin 1973).

Work by Bill Libby and colleagues, based on the properties of stump sprouts in species that coppice, proved it was possible to delay maturation and the associated loss of rootability and vigour (Libby *et al.* 1972; Eldridge and Owen 1988). This is achieved by hedging that keeps the production of new shoots close to the seedlings' original root collar, which also avoids needing to collect cuttings from well above ground level. It can also be achieved by serial propagation, producing cuttings from small seedlings, and then repropagating from such cuttings while they are still small. Many variations of this approach of propagating from shoots close to the base of the original seedlings have since proved possible (Menzies *et al.* 1988). This makes 'family forestry', in the form of deploying particular families in block plantings, easy to do.

A key outcome of hedging of juvenile material has been easy and reasonably cheap use of nursery cuttings to extend pilot quantities of seed of top genetic quality. Such use of vegetative multiplication began in the early 1980s and has been widely used operationally to accelerate the capture of genetic gain (Menzies *et al.* 1992). An alternative technology for multiplying seedling material, based on in-vitro tissue culture, was developed from the late 1970s by Kathy Horgan with further development by Jenny Aitken-Christie and Dale Smith (Hargreaves and Menzies 2007). This technology was subsequently taken up by Tasman Forestry under the leadership of John Gleed, although the planting stock remained quite expensive to produce and still subject to maturation.

Full clonal forestry, involving large-scale deployment of a limited number of well-proven clones, has long been an ideal, but has been severely hampered in *P. radiata* until recently by imperfect control of maturation (Miller 1991). Although hedging was successful in delaying maturation and thereby facilitating vegetative multiplication, hedging could never outright halt maturation. Cold storage of tissue cultures was researched and found not to be a solution, largely because tissue cultures continued to mature during the necessary sub-culturing process. Moreover, despite significant research, actual rejuvenation of vegetative material has remained just a goal.

Embryogenesis combined with cryopreservation provides a solution to controlling maturation, thereby permitting true clonal forestry (Smith *et al.* 1994; Menzies and Aimers-Halliday 2004). Cryopreservation of embryogenic material offers both a complete halt to maturation and relatively cheap storage of clonal material. While 'capture' of clones across various *P. radiata* families has been disappointing (averaging around 10–13% — although some clones have been propagated from every family), recent research results are showing much higher capture rates (C.L. Hargreaves, *pers. comm.*, 2008).

There are now two commercial producers of clonal 'varieties' of *P. radiata* in New Zealand (cf. Sorensson and Shelbourne 2005): ArborGen Australasia Ltd (who have a collaborative relationship with Scion), and Forest Genetics CellFor Ltd (affiliated with Forest Genetics Ltd), both based on the embryogenesis–cryopreservation approach. Use of clones is poised to expand significantly in New Zealand and Australian plantation estates.

Progress in developing the in-vitro propagation technology has included continuing research on cryopreservation of cotyledon and axillary-shoot material, and has been reviewed by Hargreaves and Menzies (2007). Initial collection of material is far easier than for embryogenesis. Use of cotyledons currently gives much the better genotype capture, but is subject to more problems associated with maturation effects.

Clones as a research tool

Using clonal material gives inherently much more precise and varied quantitative genetic information than seedling families (Burdon and Shelbourne 1974), but results can be subject to bias from epigenetic effects associated with clonal propagation. Such information is assuming greater interest in the light of moves towards clonal forestry, the tentative adoption of cloning in the breeding population, and quest for better characterisation of patterns of genotype-site interaction. For the most part, juvenile clonal material has given results broadly consistent with those from seedlings (Burdon *et al.* 1992b; Kumar *et al.* 2008; Baltunis *et al.* in press), but indicating markedly higher broad-sense than narrow-sense heritability for growth rate.

Institutional developments

A key factor in the development of the breeding program was the presence of a single large institution in the Forest Research Institute (FRI) within the national Forest Service.

Within FRI

The initial divide between operational breeding and research within FRI came to an end with the arrival of new scientists, notably Geoff Sweet, Rowland Burdon and Tony Shelbourne. The process of combining the two, which was informal, was essentially complete by 1968. Geoff Sweet specialised in work relating to seed orchards, reproductive biology and vegetative propagation in general, while Martin Bannister and Rowland Burdon retained a focus on base populations and genetic resources. John Miller, Tony Firth, Gerry Vincent and Charlie Low played major roles in the operational program, as well as strong supporting roles to research.

The tree improvement program benefited further from the addition of several well-trained scientists; during the 1970s these were Mike Wilcox and Mike Carson, followed by Sue Carson in 1982, and 2–4 year inputs by both John King and Randy Johnson in the late 1980s. Paul Jefferson, Keith Jayawickrama and Charles Sorensson began their contributions during the 1990s, followed by Luis Gea and subsequently Satish Kumar and Heidi Dungey. Strong and continuing operational and technical contributions during this period have come from a large group, including Mark Miller, Toby Stovold and Ruth McConnochie.

From early days collaboration occurred between the breeders and geneticists and other groups within FRI. Determination of wood properties, for characterising plus trees and researching inheritance, was led by John Harris. Physiological research for seed-orchard development, rooting cuttings and in-vitro propagation depended on collaboration led by Roger Cameron with Geoff Sweet's program. Other collaboration involved Soils and Nutrition personnel and forest pathologists, and later growth modellers and pulp and paper scientists.

Organisational changes occurred. They meant that study of vegetative propagation for producing commercial planting stock under Mike Menzies, and study of the performance of improved breeds under Mike Carson, which proceeded for some years in a separate division, were brought together in 1990. In 1992, with the creation of a Crown Research Institute, the fledgling program of molecular biology, focused on DNA mapping, gene expression and genetic engineering, was brought together with the genetics and breeding work in a Biotechnology Division under Mike Carson.

Involvement of industry

While the genetic improvement program was run from FRI since 1951, there was also early involvement by private companies. Personnel from NZ Forest Products Ltd had been taking an interest in plus tree selection even before the breeding program was set up, and later, although the commitment was sporadic, supported a search for *Dothistroma*-resistant candidates in the 1960s. Subsequently, Tasman Forestry Ltd set up its own seed orchard, on a warm, low-altitude site, which provided a good source of research information. Their orchard work was followed by a commitment in 1983 to set up a laboratory for mass-scale tissue-culture propagation, and (under their various subsequent names) later involvement in a range of propagation technologies.

In 1965, at the instigation of Dr Dennis Richardson, Director of Research, an FRI symposium was held on 'The improvement of *Pinus radiata*', with Prof. Bruce Zobel of North Carolina as a visiting participant. At the symposium came an insistent demand from industry for the 'multinodal' or (short-internode) branching habit (Burdon and Thulin 1966). From around that time liaison between FRI and industry was maintained by a Research Advisory Committee, involving both the Forest Service Conservancies and the main companies, a mechanism that generally worked very harmoniously. Subsequently, in the 1990s, an industry–research advisory board (FAFPRO) provided a similar liaison role.

After largely withdrawing from involvement in genetic improvement of the species, NZ Forest Products Ltd renewed their involvement with the establishment of seed orchards and

family trials, and (as Carter Holt Harvey) started their own clonal program.

Relationships with Australia

From very early there was communication between FRI personnel and Australian breeders and researchers, helped by a trans-Tasman Research Officers' Exchange Scheme. Another factor was the regular attendance of a New Zealand observer at the Australian Forestry Council Research Working Group 1 (Genetics) meetings. Research material had been exchanged across the Tasman, and many of the 850-series clones, and subsequently, 268 crosses and 880-series clones, had been made available to Australian breeding programs. Relationships with individual tree breeders and forest geneticists in Australia were generally cordial, but practical collaboration was often hampered by high-level divisions among the states and general divisions between states and CSIRO.

The decision by state of New South Wales to join the New Zealand Radiata Pine Breeding Cooperative (see later) in 1990 was a major development (Johnson *et al.* 2008), and was in recognition both that selections made in New Zealand often performed very well in the state, and that NZ producers (notably Proseed Ltd) had the ability to provide large quantities of high-quality improved seed.

Collaboration with the Southern Tree Breeding Association, based in South Australia, and which was formed in the early 1980s, has occurred in a number of joint projects, including the CONSERVE strategy aimed at the protection of native-population resources, and the IMPACT project, aimed at jointly supporting screening of NZ, Australian and Chilean breeding parents for resistance to pine pitch canker (PPC). However, collaboration in the form of exchanges and coordinated management of genetic material has been constrained by the competitive relationship that was imposed by the commercial models that developed on both sides of the Tasman Sea.

Relationships with other countries

It was logical to also have relationships with personnel from California, the natural home for the species. Indeed, a key contact over the years was Professor Bill Libby, of University of California, Berkeley, from 1964 onwards. He was involved in seed-collecting expeditions to Guadalupe and Cedros Islands in 1964 and 1978, and took sabbatical leave in Rotorua in 1971 and 1991–1992, with visits in between, as well as spending several years on contract in retirement with the Tasman Forestry/Fletcher Challenge tissue culture–clonal forestry operation at Te Teko in the Bay of Plenty during 1989–2002. Exchanges of ideas on breeding strategy, genetic conservation and clonal forestry continued almost throughout.

Linkages with North Carolina State University, with its major quantitative genetics base, have been strong and various. Five scientists who have worked in the program took their doctorates at the Forestry School there. That helped inculcate an awareness of the parallels between tree breeding and animal breeding. There was also the ongoing influence of and communication with Gene Namkoong of the Genetics Department. Other universities, however, have contributed to a diversity of training backgrounds.

Various other overseas scientists contributed in the course of sabbaticals, and many overseas breeders assisted during training visits.

Relationships with Chile, the other main grower of *P. radiata*, developed slowly. In 1972–1973, Martin Bannister, as a IUFRO Working Party chairman, made a visit to obtain genetic samples of stands. The seed collection was made, despite the turmoil of the later days of the Allende regime, but the material never arrived in New Zealand. In 1978, soon after a breeding program was restarted along the lines of the North Carolina breeding cooperative model, Rowland Burdon acted as an FAO consultant, with a follow-up visit to New Zealand by Chilean breeders. Tony Shelbourne also carried out a consultancy in 1994, for an overhaul of the Chilean breeding program. Since then, New Zealand relationships with improvement operations in Chile have largely focussed on:

- transfer of vegetative propagation technology
- the joint IMPACT project, researching pine pitch canker resistance
- staff exchanges at the technical level.

The ‘cultural revolution’ and its aftermath

The break-up of the NZ Forest Service in 1987 was part of sweeping institutional and economic reforms in NZ. FRI was left as the largest unit within a rump organisation called the Ministry of Forestry, which otherwise had only policy-related and regulatory roles. The Forest Service commercial arm, in the form of the exotic plantations and sawmills, became a state-owned enterprise called New Zealand Timberlands, within which Proseed was created as the manager of the seed orchards and seed store. At the same time, the state research organisations began to be required to raise some of their funding from industry, on a regime of user-pays (Burdon and Carson 2000). Development of several industry–research cooperatives soon followed (S. Carson 1990), including the formal setting up of the New Zealand Radiata Pine Breeding Cooperative (RPBC) in 1988. This was a fraught process, with companies being asked for the first time to make direct contributions to research funding.

Other organisations were subsequently formed between FRI and industry, including SORG (a seed orchard research group), and GEENZ which had a focus on biotechnology research, but both were relatively short-lived.

Further change to the FRI came in 1992, when it became a stand-alone Crown Research Institute, operating as a company and expected to build and market its own intellectual property (IP) as a trading asset. However (and not surprisingly), this conflicted with various of the funding arrangements struck since 1987, notably with the RPBC, thereby constraining FRI’s ability to appropriate and market breeding IP. Some companies also began marketing their own breeding IP, instead of being purely clients of the breeding program.

In 1992 there was also major privatisation of former state forests, and another major privatisation occurred in 1996, centring on the sale of the Kaingaroa Forest. Continuing changes in ownership and management of forests (which are part of an international pattern) have contributed to complications in moving the breeding program forward, as well as contributing to losses of

some important progeny trials. However, the privatisation also introduced important new players into the NZ forestry sector, which underscored the need to accommodate diverse breeding goals and for an overall boost of funding support for the tree breeding program.

Further change came in 2001, with RPBC becoming a limited liability company, driven by the need for the increasing proportion of industry funding to be managed under a more business-oriented, legal entity. Mike Carson concluded 16 years of leading the breeding program, then the FRI Division containing it, and then the RPBC, by implementing a dictate of the Foundation for Research, Science and Technology (FRST). This entailed promoting and achieving formation of a consortium (end of 2004), within the FRST Industrial Research Program, representing the RPBC, consisting of industry company shareholders and the FRI (which had then become *Forest Research* and then Scion represented briefly by Ensis Genetics), in a situation that is continuing to evolve. The continuing challenges of successfully integrating industry needs with those of research providers to the RPBC need to be considered in the context that industry shareholders now contribute almost 50% of the \$2 million per year spent on developing the tree improvement program.

In parallel, another FRST consortium, the Wood Quality Initiative (WQI — now the Solid Wood Initiative) was set up in 2002 between industry and research providers to study and solve problems with wood quality in *P. radiata*, with a consistent emphasis on supporting genetic improvement. The recent establishment of Future Forests Research Ltd (www.ffr.co.nz) has completed the industry–research consortium coverage of New Zealand’s plantation forestry sector, and it is expected to provide important linkages between the tree improvement program and subsequent forest-growing R&D.

These institutional changes have led to a mixed picture. On the one hand, the genetic management of breeding has tended to assume a shorter-term focus and a task-by-task decision-making process. On the other hand, there has been a greater industry involvement in tree improvement decision-making, as well as a move into more fundamental research into wood formation and wood properties, with an important emphasis on studying gene expression. The molecular work, however, has so far intersected with operational breeding only in the use of DNA markers to verify clonal identity and pollen parentage, with further potential yet to be fulfilled.

Concluding

The breeding program represents an important case history of the domestication of forest trees. Yet, in the genetic sense, the species is still very close to the wild state. Much of the current genetic improvement amounts, in effect, to ‘making good’ losses in both overall yields and log- and wood quality resulting from management practices designed to enhance clearwood production and reduce effective growing costs. Certain of the most easily captured genetic gains, involving tree form and growth rate, have clearly been achieved, and further such gains should be achievable. In addition, progress has been made in resistances to diseases including *Dothistroma* and *Cyclaneusma* needle-casts, as well as in developing strategies to minimise future losses

to pathogens. Also, various advances in technology are now facilitating genetic improvement in wood properties which have hitherto been far more difficult to address. All such research needs to continue with an eye to managing various risk factors.

A cautionary tale exists in the ease and rapidity with which advancement of the breeding population can lead to narrowing of its genetic base, unless strong countermeasures are taken.

Being able to use controlled crossing to deliver genetic gain, through better technologies for seed orchards and or mass vegetative propagation, has been important. It gives quicker and better capture of genetic gain, and has allowed better structuring of the breeding population. Yet the availability of pedigree reconstruction could avert much of the logistical and physical effort of controlled pollination within the breeding population.

Challenges remain in perfecting clonal forestry with the species, but this will make accessible gains that depend on intermediate optima for certain traits. Clonal forestry offers the prospect of capturing gains in crop performance that are independent of competitive ability, which would take domestication to a new level.

Targeting breeding goals is an ongoing challenge, especially with the relatively complex production systems. DNA technology offers the prospect of refining population management, selection among candidates, and extending the range of feasible goals.

Managing risk, while pursuing intensive genetic gain, is always a challenge. It will depend heavily on good management of the populations needed for long-term breeding. Yet, with the availability of much-improved stock, and the direct costs and opportunity costs of maintaining a full infrastructure of genetic resources, there are great temptations to neglect important aspects of population management. Resisting such temptations will be doubly challenging in the context of changing institutional structures.

While the successes have been great, there is no cause for complacency. Maintaining technical capability, and achieving continued and well-targeted genetic gain while managing the risks, will all be needed to safeguard the competitive ability of this important sector of the national economy.

Acknowledgements

Various individual contributions, especially certain of the major ones, have been mentioned explicitly and or in literature citations. Less than duly acknowledged thereby are, in particular, the contributions of Mike Wilcox who became leader of the program and then of a Division within FRI. Emphasis has necessarily been on historical achievements, rather than work still in progress. In addition, there have been the crucial cumulative contributions made by a great many others who have over the years been involved in the program. Specific thanks are due to Charlie Low for help in drawing up Table 1, Satish Kumar and Mike Menzies for some helpful suggestions and corrections, Keith Jayawickrama for checking accuracy, Alan Brown for some suggestions, and Ken Eldridge for some corrections in the referencing.

References

- Aimers-Halliday, J. and Burdon, R.D. (2003) Risk management for clonal forestry with *Pinus radiata*: analysis and review. 2: Technical and logistical problems and countermeasures. *New Zealand Journal of Forestry Science* **33**, 181–204.
- Axelrod, D.I. (1980) *History of Maritime Closed-Cone Pines: Alta and Baja California*. University of California Publications in Geological Science, Vol. 120, 143 pp.
- Baltunis, B.S., Wu, H.X., Dungey, H.S., Mullin, T.J. and Brawner, J.T. (in press) Comparison of genetic parameters and clonal value predictions from clonal trials and seedling base population trials of radiata pine. *Tree Genetics and Genomics*. (Online First)
- Bannister, M.H. (1959) Artificial selection and *Pinus radiata*. *New Zealand Journal of Forestry* **8**, 69–90.
- Bannister, M.H. and McDonald, I.R.C. (1983) Turpentine composition of the pines of Guadalupe and Cedros Islands. *New Zealand Journal of Botany* **21**, 373–377.
- Beauregard, R., Gazo, R., Kimberley, M.O., Turner, J.C.P., Mitchell, S.A. and Shelbourne, C.J.A. (1999) Genotype variation in radiata pine random width board quality. In: Zhang, S.Y., Gosselin, R. and Chauret, G. (eds) *Timber Management toward Wood Quality and End-Product Value*. Proceedings of CTIA/IUFRO International Wood Quality Workshop, Quebec, August 1997. Chapter IV, pp. 53–62.
- Burdon, R.D. (1977) Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. *Silvae Genetica* **26**, 168–175.
- Burdon, R.D. (1979) Generalisation of multi-trait selection indices using information from several sites. *New Zealand Journal of Forestry Science* **22**, 145–152.
- Burdon, R.D. (1986) Clonal forestry and breeding strategies — a perspective. In: *Proceedings, IUFRO Genetics Group Meeting*. Williamsburg, VA, October 1986, pp. 645–659.
- Burdon, R.D. (1992) Genetic survey of *Pinus radiata*. 9: General discussion and implications for genetic management. *New Zealand Journal of Forestry Science* **22**, 274–398.
- Burdon, R.D. (2001) *Pinus radiata*. In: Last, F.T. (ed.) *Ecosystems of the World. Vol. 19: Tree Crop Ecosystems*. Elsevier, Amsterdam, The Netherlands, pp. 99–161.
- Burdon, R.D. and Aimers-Halliday, J. (2003) Risk management for clonal forestry with *Pinus radiata*: analysis and review. 1: Strategic issues and risk spread. *New Zealand Journal of Forestry Science* **33**, 156–180.
- Burdon, R.D. and Carson, M.J. (2000) Conservation and management of genetic resources of commercial forests in New Zealand: Challenges of institutional changes and new technology. In: Mátyás, C. (ed.) *Forest Genetics and Sustainability*. Kluwer, Dordrecht, The Netherlands, pp. 235–246.
- Burdon, R.D. and Shelbourne, C.J.A. (1971) Breeding populations for recurrent selection: conflicts and possible solutions. *New Zealand Journal of Forestry Science* **1**, 174–193.
- Burdon, R.D. and Shelbourne, C.J.A. (1974) The use of vegetative propagules for obtaining genetic information. *New Zealand Journal of Forestry Science* **4**, 418–425.
- Burdon, R.D. (compil.) and Thulin, I.J. (ed.) (1966) *The Improvement of Pinus radiata*. Proceedings of New Zealand Forest Service, Forest Research Institute Symposium No. 6, 92 pp.
- Burdon, R.D. and Walter, C. (2004) Exotic pines and eucalypts: perspectives on risks of transgenic plantations. In: Strauss, S.H. and Bradshaw, H.D. (eds) *The Bioengineered Forest: Challenges for Science and Society*. RFF Press, Washington, DC, pp. 52–75.
- Burdon, R.D. and Wilcox, P.L. (2007) Population management: potential impacts of advances in genomics. *New Forests* **34**, 187–206.

- Burdon, R.D., Shelbourne, C.J.A. and Wilcox, M.D. (1978) Advanced selection strategies. In: *Proceedings of 3rd World Consultation on Forest Tree Breeding*. Canberra 1977, Vol. 2, pp. 1133–1147.
- Burdon, R.D., Currie, D. and Chou, C.K.S. (1982) Response to inoculation with *Diplodia pinea* in progenies of apparently resistant trees of *Pinus radiata*. *Australasian Plant Pathology* **11**, 37–39.
- Burdon, R.D., Bannister, M.H. and Low, C.B. (1992a) Genetic survey of *Pinus radiata*. 2: Variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings. *New Zealand Journal of Forestry Science* **22**, 138–159.
- Burdon, R.D., Bannister, M.H. and Low, C.B. (1992b) Genetic survey of *Pinus radiata*. 4: Variance structures and heritabilities in juvenile clones. *New Zealand Journal of Forestry Science* **22**, 187–210.
- Burdon, R.D., Bannister, M.H. and Low, C.B. (1992c) Genetic survey of *Pinus radiata*. 5: Between-trait and age-age correlations for growth rate. *New Zealand Journal of Forestry Science* **22**, 211–227.
- Burdon, R.D., Broekhuizen, P. and Zabkiewicz, J.A. (1997a) Comparison of native-population and New Zealand land-race samples of *Pinus radiata* using cortical monoterpenes. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua. FRI Bulletin No. 203, pp. 50–56.
- Burdon, R.D., Firth, A., Low, C.B. and Miller, M.A. (1997b) Native provenances of *Pinus radiata* in New Zealand: performance and potential. *New Zealand Journal of Forestry* **41**, 32–36.
- Carson, M.J. (1986a) Control-pollinated seed orchards of best general combiners — a new strategy for radiata pine improvement. In: Wratt, G. (ed.) *Agronomy Society of New Zealand Special Publication No. 5*, pp. 144–148.
- Carson, M.J. (1986b) Advantages of clonal forestry for *Pinus radiata* — real or imagined? *New Zealand Journal of Forestry Science* **16**, 403–415.
- Carson, M. (1988) *Long-Internode or Multinodal Radiata Pine — A Financial Analysis*. New Zealand Ministry of Forestry, FRI Bulletin No. 115, 25 pp.
- Carson, M.J. (1989) Comparison of improved radiata pine breeds using STANDPAK. In: James, R.N. and Tarlton, G.L. (eds) *New Approaches to Spacing and Thinning in Plantation Forestry*. Proceedings of IUFRO Symposium, Rotorua, New Zealand. Ministry of Forestry, FRI Bulletin No. 151, pp. 184–194.
- Carson, M.J. (1997) FRI research on genetic diversity, as a component of biodiversity of forests. *New Zealand Journal of Forestry* **42**, 14–16.
- Carson, M.J. and Burdon, R.D. (1991) Relative advantages of clonal forestry and vegetative multiplication. In: Miller, J.T. (ed.) *Proceedings of FRI/NZFP Forests Ltd Clonal Forestry Workshop*. 1–2 May 1999, Rotorua, New Zealand. Ministry of Forestry, FRI Bulletin No. 160, pp. 41–43.
- Carson, M.J. and Inglis, C.S. (1989) Genotype and location effects on internode length of *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* **18**, 267–279.
- Carson, M.J., Tombleson, J.D. and Wilcox, P.L. (1991) Research for stand management of clones. In: Miller, J.T. (ed.) *Proceedings of FRI/NZFP Forests Ltd Clonal Forestry Workshop*. 1–2 May 1999, Rotorua, New Zealand. Ministry of Forestry, FRI Bulletin No. 160, pp. 147–149.
- Carson, M.J., Vincent, T.G. and Firth, A. (1992) Control-pollinated and meadow seed orchards of radiata pine. In: *Mass Production Technology for Genetically Improved Fast Growing Forest Tree Species*. Proceedings of IUFRO Conference, Bordeaux, France, September 1992. AFOCEL, Nangis, France. Vol. **II**, 13–20.
- Carson, M.J., Walter, C. and Carson, S.D. (2004) The future of forest biotechnology. In: Kellison, R., McCord, S. and Gartland, K.M.A. (eds) *Forest Biotechnology in Latin America*. Institute of Forest Biotechnology, Raleigh, NC, USA. ISBN 0-9763838-0-2, pp.13–38.
- Carson, M.J., Carson, S.D., Richardson, T.E., Walter, C., Wilcox, P.L., Burdon, R.D. and Gardner, R.C. (1996) Molecular biology applications to forest trees — fact or fiction? In: Dieters, M.J., Matheson, A.C., Nikles, D.G., Harwood, C.E. and Wright, S.M. (eds) *Tree Improvement for Sustainable Tropical Forestry*. Proceedings of QFRI – IUFRO Conference, Caloundra, Queensland, Australia, 27 October–1 November 1996. Queensland Forestry Research Institute, Gympie, pp. 272–281.
- Carson, S.D. (1990) FRI/Industry Research Co-operatives — a framework for successful collaboration. *New Zealand Journal of Forestry* **34**, 14–17.
- Carson, S.D. (1991) Genotype × environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* **21**, 32–49.
- Carson, S.D. (1996) Greater specialisation of improved seedlots: new developments for efficient selection of parents and evaluation of performance. *New Zealand Journal of Forestry* **41**, 12–17.
- Carson, S.D. and Carson, M.J. (1986) A breed of radiata pine resistant to dothistroma needle blight. In: Wratt, G. (ed.) *Agronomy Society of New Zealand Special Publication No. 5*, pp. 202–207.
- Carson, S.D. and Carson, M.J. (1989) Breeding for resistance in forest trees — a quantitative genetic approach. *Annual Review of Phytopathology* **27**, 373–395.
- Carson, S.D., García, O.P. and Hayes, J.D. (1999a) Realised gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *Forest Science* **45**, 186–200.
- Carson, S.D., Kimberley, M.O., Hayes, J.D. and Carson, M.J. (1999b) The effect of silviculture on genetic gain in growth of *Pinus radiata* at one-third rotation. *Canadian Journal of Forest Research* **29**, 1979–1984.
- Cotterill, P.P. (1989) The nucleus breeding system. In: *Proceedings of 20th Southern Forest Tree Improvement Conference*. Charleston, SC, USA, pp. 36–42.
- Cown, D.J. (1992) Corewood (juvenile wood) in *Pinus radiata* — should we be concerned? *New Zealand Journal of Forestry Science* **22**, 87–95.
- Dickson, R.L. (1996) Seed production in *Pinus radiata* D.Don: impact of climate and site on numbers of emerging female strobili. PhD thesis, University of Canterbury, New Zealand, xxiv + 317 pp.
- Donaldson, L.A., Croucher, M. and Uprichard, J.M. (1995) Clonal variation of wood chemistry variables in radiata pine (*Pinus radiata* D.Don). *Holzforchung* **51**, 537–542.
- Dungey, H.S., Carson, M.J., Low, C.B. and King, N.G. (2004) Potential and niches for inter-specific hybrids with *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* **33**, 295–318.
- Dungey, H.S., Matheson, A.C. and Evans, R. (2006) Genetics of wood stiffness and its component traits in *Pinus radiata*. *Canadian Journal of Forest Research* **36**, 1165–1178.
- Dungey, H.S., Brawner, J.T., Burger, F., Carson, M., Henson, M., Jefferson, P. and Matheson, A.C. (in press) A new direction for the *Pinus radiata* breeding strategy for the Radiata Pine Breeding Company. *Silvae Genetica*.
- Dungey, H.S., Low, C.B., Ledgard, N.J. and Stovold, G.T. (in MS) An alternative to *Pinus radiata* in some New Zealand high country: survival, early growth and snow resistance of *P. attenuata*, *P. radiata* and F1 hybrids.
- Eldridge, K.G. (1978) Seed collections in California in 1978. *CSIRO Division of Forest Research Annual Report, 1977–1978*, pp. 8–17.
- Eldridge, K.G. and Owen, J.N. (1988) Production methods for cuttings in Australia. In: Menzies, M.I., Aimers, J.P. and Whitehouse, L.J. (eds) *Proceedings of Workshop on Growing Radiata Pine from Cuttings*. New Zealand Ministry of Forestry, FRI Bulletin No. 135, pp. 99–107.

- Elwes, H.J. and Henry, A. (1910) *The Trees of Great Britain & Ireland*, Vol. 5. Privately published in Edinburgh.
- Evans, R., Kibblewhite, R.P. and Lausberg, M.F. (1999) Relationships between wood and pulp properties of twenty-five 13-year-old radiata pine trees. *Appita Journal* **52**, 132–139.
- Field, J.F. (1934) Experimental growing of insignis pine from slips. *New Zealand Journal of Forestry* **3**, 195.
- Fielding, J.M. (1953) *Variations in Monterey Pine*. Forestry and Timber Bureau, Canberra, Bulletin No. 31, 43 pp.
- Fielding, J.M. (1954) *Methods of Raising Monterey Pine from Cuttings in the Open Nursery*. Forestry and Timber Bureau, Canberra, Bulletin No. 32, 29 pp.
- Fielding, J.M. (1961a) *Provenances of Monterey and Bishop Pines*. Forestry and Timber Bureau, Canberra, Bulletin No. 38, 30 pp.
- Fielding, J.M. (1961b) The pines of Cedros Island. *Australian Forestry* **24**, 62–65.
- Franich, R.A., Carson, S.D. and Carson, M.J. (1986) Synthesis and accumulation of benzoic acid in *Pinus radiata* tissues in response to tissue injury by dothistromin, and correlation of resistance of *P. radiata* families to *Dothistroma pini*. *Physiological Plant Pathology* **28**, 267–286.
- Gea, L.D., Lindgren, D., Shelbourne, C.J.A. and Mullin, T.J. (1997) Complementing inbreeding coefficient information with status number: implications for structuring breeding populations. *New Zealand Journal of Forestry Science* **27**, 255–271.
- Gea, L.D., Dungey, H.S. and Low, C.B. (2006) Inter- and intra-specific hybrids with radiata pine: what can they add? In: Mercer, C.F. (ed.) *Breeding for Success, Diversity in Action*. Proceedings of 13th Australasian Plant Breeding Conference, April 2007, Christchurch, New Zealand, www.apbc.org.nz, pp. 911–917.
- Hargreaves, C. and Menzies, M. (2007) Organogenesis and cryopreservation of juvenile radiata pine. In: Jain, S.M. and Häggman, H. (eds) *Protocols for Micropropagation of Woody Trees and Fruits*. Springer, pp. 51–65.
- Ivković, M., Kumar, S. and Wu, H.X. 2006. Adding value to the end-products of radiata pine: Review of breeding for structural timber production. In: Mercer, C.F. (ed.) *Breeding for Success, Diversity in Action*. Proceedings of 13th Australasian Plant Breeding Conference, April 2007, Christchurch, New Zealand, www.apbc.org.nz, pp. 273–278.
- Jacobs, M.R. (1939) *The Vegetative Propagation of Forest Trees. 1. Experiments with Cuttings of Pinus radiata D. Don*. Commonwealth Forestry Bureau, Australia, Bulletin No. 25, 30 pp.
- Jayawickrama, K.J.S. and Carson, M.J. (2000) A breeding strategy for the New Zealand Radiata Pine Breeding Cooperative. *Silvae Genetica* **49**, 82–90.
- Jayawickrama, K.J.S., Shelbourne, C.J.A. and Carson, M.J. (1997a) New Zealand's long-internode breed of *Pinus radiata*. *New Zealand Journal of Forestry Science* **27**, 126–141.
- Jayawickrama, K.J.S., Carson, M.J., Jefferson, P.A. and Firth, A. (1997b) Development of the New Zealand radiata pine breeding population. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. FRI Bulletin No. 203, pp. 217–226.
- Johnson, I.G. (1992) Family–site interaction in radiata pine families in NSW, Australia. *Silvae Genetica* **41**, 55–62.
- Johnson, G.R. and Burdon, R.D. (1990) Family–site interaction in *Pinus radiata*: implications for progeny testing strategy and regionalised breeding in New Zealand. *Silvae Genetica* **39**, 55–62.
- Johnson, I.G., Ades, P.K. and Eldridge, K.G. (1997) Growth of natural Californian provenances of *Pinus radiata* in New South Wales, Australia. *New Zealand Journal of Forestry Science* **27**, 23–38.
- Johnson, I.G., Cottrell, I.M., Raymond, C.A. and Henson, M. (2008) Half a century of *Pinus radiata* improvement in NSW. *New Zealand Journal of Forestry* **52**, 7–13.
- Kibblewhite, R.P. and Shelbourne, C.J.A. (1997) Genetic selection of trees with designer fibres for different paper and pulp grades. In: *Fundamentals of Papermaking Materials*. Transactions of 11th Fundamental Research Symposium, Cambridge, UK, September 1997, pp. 439–472.
- King, J.N. and Burdon, R.D. (1991) Time trends in inheritance and projected efficiencies of early selection in a large 17-year-old progeny test of *Pinus radiata*. *Canadian Journal of Forest Research* **21**, 1200–1207.
- Kube, P. and Carson, M. (2004) A review of risk factors associated with clonal forestry of conifers. In: Walter, C. and Carson, M. *Plantation Biotechnology for the 21st Century*. Research Signpost, Trivandrum, Kerala, India, pp. 337–361.
- Kumar, S. (2004a) Effect of selfing on various economic traits in *Pinus radiata* and some implications for breeding strategy. *Forest Science* **50**, 571–578.
- Kumar, S. (2004b) Genetic parameter estimates for wood stiffness, strength, internal checking and resin bleeding for radiata pine. *Canadian Journal of Forest Research* **34**, 2601–2610.
- Kumar, S., Dungey, H. and Matheson, A.C. (2006) Genetic parameters and strategies for genetic improvement of stiffness in radiata pine. *Silvae Genetica* **34**, 77–84.
- Kumar, S., Gerber, S. and Richardson, T.E. (2007a) Pedigree reconstruction using SSR markers in a radiata pine breeding programme. In: Mercer, C.F. (ed.) *Breeding for Success, Diversity in Action*. Proceedings of 13th Australasian Plant Breeding Conference, April 2007, Christchurch, New Zealand, www.apbc.org.nz, pp. 578–592.
- Kumar, S., Gerber, S., Richardson, T.E. and Gea, L.D. (2007b) Testing for unequal parental contributions in using nuclear and chloroplast SSR markers in polycross families of radiata pine. *Tree Genetics and Genomes* **3**, 207–214.
- Kumar, S., Burdon, R.D. and Stovold, G.T. (2008) Wood properties and stem diameter of radiata pine in New Zealand: genetic parameter estimates compared between seedling and clonal material. *New Zealand Journal of Forestry Science* **38**, 88–101.
- Libby, W.J. (1973) Domestication strategies for forest trees. *Canadian Journal of Forest Research* **3**, 265–276.
- Libby, W.J., Brown, A.G. and Fielding, J.M. (1972) Effects of hedging radiata pine on production, rooting and early growth of cuttings. *New Zealand Journal of Forestry Science* **2**, 263–283.
- Low, C. and Smith, T. (1997) Use of Guadalupe provenance in *Pinus radiata* improvement in New Zealand. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua. FRI Bulletin No. 203, pp. 57–61.
- Low, C.B., Dungey, H.S., Powell, M. and Miller, M.A. (2006) Growth and genetic gains from seed-orchard seedlots of *Pinus radiata* in a trans-Tasman study. In: Mercer, C. (ed.) *Breeding for Success, Diversity in Action*. Proceedings of 13th Australasian Plant Breeding Conference, Christchurch, New Zealand, April 2006. www.apbc.org.nz, pp. 442–450.
- MAF (2007) *A National Exotic Forest Description as at April 2007*. Ministry of Agriculture and Forestry, Wellington, 62 pp.
- Matheson, A.C. and Raymond, C.A. (1984) The impact of genotype × environment interactions on Australian *Pinus radiata* breeding programs. *Australian Forest Research* **14**, 11–35.
- Menzies, M.I. and Aimers-Halliday, J. (2004) Propagation options for clonal forestry with conifers. In: Walter, C. and Carson, M. (eds) *Plantation Biotechnology for the 21st Century*. Research Signpost, Trivandrum, Kerala, India, pp. 255–274.
- Menzies, M.I., Burdon, R.D., Holden, D.G. and Warrington, I.J. (1987) Family variation in frost resistance of *Pinus radiata*. *New Forests* **1**, 171–186.

- Menzies, M.I., Aimers, J.P. and Whitehouse, L.J. (eds) (1988) *Proceedings of Workshop on Growing Radiata Pine from Cuttings*. New Zealand Ministry of Forestry, FRI Bulletin No. 135.
- Menzies, M.I., Faulds, T. and Dibley, M.J. (1992) Production of radiata pine cuttings for plantation forestry in New Zealand. *Acta Horticulturae* **319**, 359–364.
- Millar, C.I. (1999) Evolution and biogeography of *Pinus radiata* with a proposed revision of its Quaternary history. *New Zealand Journal of Forestry Science* **29**, 335–365.
- Miller, J.T. (ed.) (1991) *Proceedings of FRI/NZFP Forests Ltd Clonal Forestry Workshop*. 1–2 May 1999, Rotorua, New Zealand. New Zealand Ministry of Forestry, FRI Bulletin No. 160, 200 pp.
- Ross, S.D., Bollmann, M.P., Pharis, R.P. and Sweet, G.B. (1984) Gibberellin A/4 and the promotion of flowering in *Pinus radiata*: effects of partitioning of photoassimilate within the bud during primordial differentiation. *Plant Physiology* **76**, 326–330.
- Shelbourne, C.J.A. (1969) *Tree Breeding Methods*. New Zealand Forest Service, Forest Research Institute Technical Paper No. 55, 43 pp.
- Shelbourne, C.J.A. (1970) Genetic improvement in different tree characters of radiata pine and the consequences for silviculture and utilisation. In: Sutton, W.R.J. (ed.) *Pruning and Thinning Practice*. Proceedings of FRI Symposium No. 12, 16–20 March 1970, Rotorua, New Zealand, pp. 44–58.
- Shelbourne, C.J.A. (1997) Genetics of adding value to the end-products of radiata pine. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua. FRI Bulletin No. 203, pp. 129–141.
- Shelbourne, C.J.A., Burdon, R.D., Bannister, M.H. and Thulin, I.J. (1979) Choosing the best provenances of radiata pine for different sites in New Zealand. *New Zealand Journal of Forestry* **24**, 288–300.
- Shelbourne, C.J.A., Burdon, R.D., Carson, S.D., Firth, A. and Vincent, T.G. (1986) *Development Plan for Radiata Pine Breeding*. New Zealand Forest Service, Forest Research Institute special publication, 142 pp.
- Shelbourne, C.J.A., Carson, M.J. and Wilcox, M.D. (1989) New techniques in the genetic improvement of radiata pine. *Commonwealth Forestry Review* **68**, 191–201.
- Shelbourne, C.J.A., Evans, R., Kibblewhite, R.P. and Low, C.B. (1996) Inheritance of tracheid dimensions and wood density in radiata pine. *Appita Journal* **50**, 47–50, 67.
- Shelbourne, C.J.A., Apiolaza, L.A., Jayawickrama, K.J.S. and Sorensson, C.T. (1997) Developing breeding objectives for radiata pine in New Zealand. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua. FRI Bulletin No. 203, pp. 160–168.
- Shelbourne, C.J.A., Kumar, S., Burdon, R.D., Gea, L.D. and Dungey, H.S. (2007) Deterministic simulation of gains for seedling and cloned main and elite breeding populations. *Silvae Genetica* **56**, 259–270.
- Shepherd, R.W. (1990) Early importations of *Pinus radiata* to New Zealand and distribution in Canterbury to 1885: implications for the genetic makeup of *Pinus radiata* stocks. (2 parts). *Horticulture in New Zealand* **1**, 28–35 and **1**, 33–38.
- Smith, D.R., Walter, C., Warr, A., Hargreaves, C.L. and Grace, L.J. (1994) Somatic embryogenesis joins the plantation forestry revolution in New Zealand. In: *Proceedings of Tappi Biological Sciences Symposium*. Minneapolis, USA, 3–4 October. Tappi Press, Atlanta, GA, pp. 19–29.
- Sorensson, C.T. and Shelbourne, C.J.A. (2005). Clonal forestry. In: Colley, M. (ed.) *Forestry Handbook*. 4th edn. New Zealand Institute of Forestry, Inc., pp. 92–96.
- Sorensson, C.T., Burdon, R.D., Cown, D.J., Jefferson, P.A. and Shelbourne, C.J.A. (1997) Incorporating spiral grain into New Zealand's radiata pine breeding programme. In: Burdon, R.D. and Moore, J.M. (eds) *IUFRO '97 Genetics of Radiata Pine*. Proceedings of NZFRI–IUFRO Conference 1–4 December and Workshop 5 December, Rotorua. FRI Bulletin No. 203, pp. 180–191.
- Sweet, G.B. (1973) Graft incompatibility in radiata pine in New Zealand. *New Zealand Journal of Forestry Science* **3**, 82–90.
- Sweet, G.B. and Thulin, I.J. (1969) The abortion of conelets in *Pinus radiata*. *New Zealand Journal of Forestry* **14**, 59–67.
- Sweet, G.B. and Thulin, I.J. (1973) The effect of maturation on growth and form of vegetative propagules of radiata pine. *New Zealand Journal of Forestry Science* **3**, 191–210.
- Turner, J.A. (1997a) Realised genetic gain in *Pinus radiata* from “850” seed orchard seedlots grown commercially in the central North Island, New Zealand. Part. 1. Growth. *New Zealand Journal of Forestry Science* **27**, 142–157.
- Turner, J.A. (1997b) Realised genetic gain in *Pinus radiata* from “850” seed orchard seedlots grown commercially in the central North Island, New Zealand. Part. 2. Stem quality. *New Zealand Journal of Forestry Science* **27**, 158–173.
- Uprichard, J.M., Kimberley, M.O., Foster, R.S. and Shelbourne, C.J.A. (1994) Thermomechanical pulping studies on ten *Pinus radiata* clones: the effects of wood quality on papermaking properties. In: *Proceedings of International Pan Pacific Conference*, San Diego, CA, USA, 6–9 November, pp. 83–99.
- van Buijtenen, J.P. and Burdon, R.D. (1990) Expected efficiencies of mating designs for advanced-generation selection. *Canadian Journal of Forest Research* **20**, 1648–1663.
- van Dorsser, J.C. and Faulds, T. (1991) Propagation system for the production of rooted cuttings from physiologically mature *Pinus radiata* within 2 years of field collection. *New Zealand Journal of Forestry Science* **21**, 135–143.
- Vincent, T.G. (1987) *Certification System for Forest Tree Seed and Planting Stock*. Ministry of Forestry, FRI Bulletin No. 134, 17 pp.
- Vincent, T.G. and Dunstan, J.S. (1989) *Register of Commercial Seedlots Issued by the New Zealand Forest Service*. Ministry of Forestry, FRI Bulletin No. 144, 136 pp.
- Walter, C., Carson, S.D., Menzies, M.I., Richardson, T. and Carson, M.J. (1998) Review: Application of biotechnology to forestry — molecular biology of conifers. *World Journal of Microbiology and Biotechnology* **14**, 321–330.
- Wilcox, M.D. (1983) Inbreeding depression and genetic variances estimated from self- and outcross-pollinated families of *Pinus radiata*. *Silvae Genetica* **32**, 89–96.
- Wilcox, P.L. and Carson, M.J. (1989) Reduced initial stockings using improved radiata pine. In: James, R.N. and Tarlton, G.L. (eds) *New Approaches to Spacing and Thinning in Plantation Forestry*. Proceedings of IUFRO Symposium, Rotorua, New Zealand. Ministry of Forestry, FRI Bulletin No. 151, pp. 233–242.
- Wilcox, M.D. and Thulin, I.J. (1976) Selection of *Pinus radiata* clones in New Zealand for planting from cuttings. *New Zealand Journal of Forestry* **21**, 239–247.
- Wu, H.X., Eldridge, K.G., Matheson, A.C., Powell, M.P., McRae, T.A., Butcher, T.B. and Johnson, I.G. (2007). Achievements in forest tree improvement in Australia and New Zealand: 8. Successful importation and breeding of radiata pine to Australia. *Australian Forestry* **70**, 215–225.
- Wu, H.X., Ivković, M., Gapare, W., Matheson, A.C., Baltunis, B.S., Powell, M.B. and McRae, T.A. (2008). Breeding for wood quality and profit in radiata pine: a review of genetic parameters. *New Zealand Journal of Forestry Science* **38**, 56–87.