PINUS RADIATA SELECTIONS FROM DIFFERENT REGIONS OF NEW ZEALAND DIFFER IN BRANCH HABIT, FORM, AND GROWTH RATE

K. J. S. JAYAWICKRAMA and C. B. LOW

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

(Received for publication 2 July 1998; revision 12 February 1999)

ABSTRACT

The North American provenances of *Pinus radiata* D. Don show differences in growth and form when grown in common-garden trials, but little has been reported on differentiation into regional land races as an exotic. Data at age 8 years from two large trials, each with progenies of plus-tree selections from different regions in New Zealand, were analysed for various traits. The first trial ("850") had polycross progenies of 109 parent clones, selected between 1950 and 1967 and belonging to six regional selection groups, and was planted on six sites in 1975. The second ("888") had 329 open-pollinated progenies, from 279 plus-trees selected in 1988 in six distinct regions and from clones in a Chilean seed orchard. This trial was planted on three sites in 1989.

In the "888" trial there were significant differences among seed sources for every trait except needle retention at all sites and malformation at one of the sites. The Tarawera source had the highest branch cluster frequency score, needle retention score, malformation score (least malformation), and percentage of acceptable stems. The Southland and Nelson sources had low branch cluster frequency scores. Branch cluster frequency score was the only trait for which significant seed-source effects were found across sites in the "850" trial. The lowest branch cluster frequency scores were for the Nelson and Southland sources. However, there were significant interactions between seed source and site, and at the site with the highest survival and heritabilities there were significant differences between seed sources for diameter, straightness score, branch cluster frequency score, and malformation score. On this site, the highest score for every trait assessed was for the Kaingaroa second-rotation seed source.

Two trends emerged from these studies. The first trend was of faster growth and better form for selections made in second-rotation stands in the central North Island. Given that most of the plus-trees selected and progeny tested for the New Zealand breeding population were selected on such sites, this was an encouraging result. The second trend was for lower branch cluster frequency for selections made in the South Island. Possible reasons for significant seed-source effects are better ability to select on certain sites and regions, founder effects, and natural and artificial selection.

Keywords: seed source; select trees; regional variation; diameter; straightness; acceptability; malformation; polycross; open-pollinated; *Pinus radiata*.

DEFINITIONS

climbing select: A seedlot collected by climbing and harvesting seed from the best 25 trees/ha (the largest and best-formed trees)

common-garden trial: A trial where distinct genotypes are tested in a common experiment

entries: Parents or seedlots tested in the trials (often from different sources)

internode: The section of stem between adjacent branch clusters

land race: A population of trees which has adapted to a specific environment in which it has been planted (Zobel & Talbert 1984)

polycross progeny: A control-pollinated family generated by crossing a parent with a mix of pollens

provenance: Original geographic area from which seed / propagules were collected from the wild species (Zobel & Talbert 1984)

seed source: Seed collected from plantations within a region. For this paper, regions were defined so that the range of establishment dates within a region was less than 45 years

unimproved: Without genetic improvement

INTRODUCTION

Large differences can be seen in growth rate, form, adaptability, and wood properties among provenances of forest tree species, when provenances are tested together in common-garden trials. A lot of data has been gathered on this subject, and reviewed (e.g., Zobel & Talbert 1984; Zobel *et al.* 1987; Morgenstern 1996). *Pinus radiata* is no exception, as reported by Falkenhagen (1991), Burdon (1992a), Burdon *et al.* (1992), Jayawickrama & Balocchi (1993), and Burdon, Firth, Low & Miller (1997).

In addition to provenance variation, there can be differences between seed sources of partially domesticated forest tree species. Zobel & Talbert (1984) gave the example of seed harvested from *Eucalyptus grandis* Maiden trees grown in Zimbabwe as the Zimbabwe seed source. Far less has been published on seed source variation than on provenance variation, although some studies exist. For instance, regional variation in performance is being investigated in *Pinus taeda* L. (loblolly pine) by the North Carolina State University - Industry Cooperative Tree Improvement Program (N.C.State University 1994, the Plantation Selection Seed Source study).

The New Zealand land race stocks of *P. radiata* were derived from the original native populations through a series of events (introduction to the country, early cultivation, natural and artificial selection). The first definitely known introduction of *P. radiata* to New Zealand was from England in 1859, and subsequently several importations of *P. radiata* seed and plants took place from the United States, England, and Australia (Shepherd & Cook 1988; Shepherd 1990). New Zealand evidently became self-sufficient for seed by the 1880s (Burdon 1992b). Systematic genetic improvement of this species in New Zealand dates back to the early 1950s (Burdon 1992b) with the selection of first-generation plus-trees continuing up to 1988. From reports on the development of the New Zealand breeding population (Shelbourne *et al.* 1986; Jayawickrama, Carson, Jefferson & Firth 1997), it can be seen that over 90% of the plus-tree selections (made in unimproved plantations) were made in the

volcanic plateau of the central North Island. However, several hundred plus-trees were selected in other regions of New Zealand as well, and there have been at least two comparative trials of selections from different regions. In the second of these trials, progenies from Chile were also tested.

Pinus radiata is grown in New Zealand from 36° to 46°S, from sea level to 600 m or higher, and on a variety of soil types; different natural selection pressures could therefore be exerted in different regions. The different importations of seed and plants could have been used to reforest different regions, and the history of plantation establishment was different in different regions. These factors could have contributed to regional differentiation. On the other hand, there may not have been enough time for natural selection to differentiate regional populations, or too much mixing may have taken place due to the collection of seed in one region for planting in another. For example, records show that Manawatu, and to a lesser extent Canterbury, were major seed collection regions for planting in the 1930s (Vincent & Dunstan 1989). Regions such as Canterbury (Burdon 1992b), which led in plantation establishment, presumably supplied seed to other regions, although there were also Nelson seedlots used in Canterbury in the 1950s (R.D.Burdon pers. comm.).

Given the forces working both for and against regional differentiation of *P. radiata* in New Zealand, quantifying how much did take place will shed light on the naturalisation of a key exotic forest species. Regional differentiation could also affect the selection of breeding population candidates, in that the genetic quality of the base material influences the success of a breeding programme. Data from the two trials mentioned above were therefore analysed to study the effect of selection region on growth, form, and adaptability of *P. radiata*.

SOURCES AND ENTRIES TESTED

"850"-series Polycross Trial ("850" Trial)

This trial was planted on six sites (three in the North Island, three in the South Island) in 1975, to estimate general combining ability for 109 parent clones selected between 1950 and 1967. Details of sources of the parent clones, the dates of selection, and the controls are given in Table 1. The clones were plus-trees from the first systematic selection programme in New Zealand; they were large healthy dominants, with straight stems, free of malformation and stem cones, and with small, flat-angled branches. The average selection intensity was 1 tree/ 40 ha.

All the clones were mated with a pollen mix from 10 "850"-series clones selected in the same period (nine selected in the central North Island, one near Nelson in the South Island). Controlled-pollinations were effected between 1968 and 1972. Seedlings for the North Island sites were raised in the Forest Research Institute nursery in Rotorua, with the rest raised in Rangiora (near Christchurch in the South Island). Details about the "850" series have been given by Shelbourne *et al.* (1986).

"888"-series Open-pollinated Trial ("888" Trial)

This series was conceived as the last major selection effort in plantations in New Zealand. The idea was to capture the genetic variability in the country's unimproved plantings of

TABLE 1–Entries tested in the "850" series polycross progeny trial.

Group	Number in group	Where selected / Description	Years stands were planted	Years plus-trees were selected
Seed sources				
Kaingaroa (old crop*)	18	Kaingaroa Forest Cpt 37, 50, 51, 64, 1024, 1027, 1142, 1186, 1188, 1204, 1206, 1265	1915–30	1950–63
Kinleith (old crop*)	19	Atiamuri area	1889–1924	1950
Kaingaroa (second rotation)	10	Kaingaroa Forest Cpt 1266, 1268, 1271, 1272 and 1274	1950–54	1966–67
Nelson	18	Golden Downs Forest, Rabbit Island, Braeburn plantation, Baigents Forest, 88 Valley, Quail Valley	1900–44	1950–61
Canterbury	21	Balmoral and Hanmer Forests, Heaton Rhodes Estate	1903–32	1963–64
Southland	23	Hokonui, West Tapanui, Rankleburn, Winton, Port Chalmers Borough Council, Whare Flat	1900–32	1952–64
Controls				
"850" Gwavas orchard		Open-pollinated seed orchard seedlot collected in 1972 (seedlot Wn/72/A2)		
Unimproved Kaingaroa bulk		Collected from clear felling "old crop" stands established in the 1920s and 1930s (seedlot R69/854)		

* The term "old-crop" refers to first-rotation stands planted in the early part of the twentieth century.

P. radiata, before they were replaced by stands of seed orchard origin. The 279 plus-trees in this series were selected in 1988, focussing on areas where few plus-trees had been selected previously: the north (Northland) and east (Hawke's Bay) of the North Island; Tahorakuri and Tarawera Forests in the central North Island; Tapanui district (Southland) and Nelson from the South Island (Table 2). The main emphasis during selection was on growth rate, followed by form and to a slight extent by crown health. About 427 ha were screened at a selection intensity of 1 tree/1.5 ha. The stands were then 14–40 years old. The main interest in selections in Tahorakuri Forest was due to the forest's establishment history. This area had been affected by an extensive fire in 1946, following which extremely dense natural regeneration had occurred, estimated to be as high as 400 000 seedlings/ha (MacArthur 1952). In addition to these six New Zealand groups, there were 44 open-pollinated progenies collected within a Chilean seed orchard.

Open-pollinated seed was collected from all the plus-trees, seedlings were raised at the Forest Research Institute nursery in Rotorua, and a progeny trial was established in 1989 at three locations in the North Island. The geographic regions from which both series ("850" and "888") were selected are shown in Fig. 1.

EXPERIMENTAL DESIGN

Both trials were established according to a Blocks-within-Replications design described by Schutz & Cockerham (1966). Details of this design (also known as Sets-in-Replications)

TABLE 2–Entries tested in the "888" series progeny trial.

Group	Number in group	Description / Source	Years stands were planted
Seed sources			
Tahorakuri	28	Kaimanawa Hill, Tahorakuri Forest	c. 1947
Tarawera	43	Tarawera Forest	1972
Hawke's Bay	55	Rukumoana, Waikoau and Tangoio Forests	1953–70
Nelson	49	Golden Downs Forest	1968–72
Northland	50	Morrisons Block, Carnachans Block, Mahurangi Block, Belton Farms, Mangakahia Opouteke Block, Topuni, and Tinopai	1955–74
Southland	49	Rankleburn, Conical Hills, Beaumont and Dusky Forests	1960–66
Chile	44	Seed collected by parent clone in a Chilean seed orchard owned by Forestal Arauco	
Controls			
"268" Kaingaroa orchard		Open-pollinated seed orchard seedlot collected in 1986 (seedlot 2/6/86/27).	
"850" Gwavas orchard		Open-pollinated seed orchard seedlot collected in 1987 (seedlot 3/3/87/1)	
Kaingaroa climbing select		Collected from above-average phenotypes, the best 25 trees/ha, from Kaingaroa Forest (seedlot FRI 79/2320).	

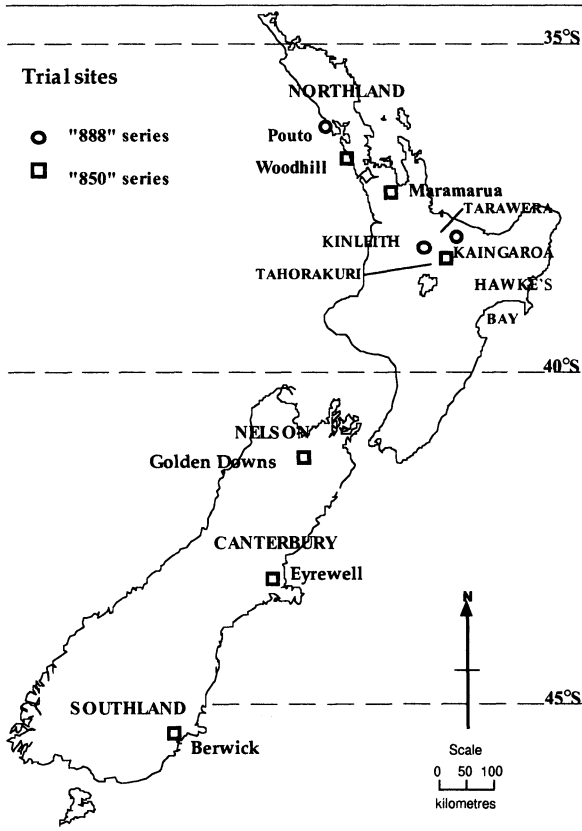

FIG. 1–Selection regions represented in the "850" series polycross and "888" series open-pollinated trials and location of trial sites. (Note: selection regions are in upper case text and trial sites are in lower case).

are given in Appendix 1. Details of the trial sites are given in Appendix 2 and the location of the trial sites is shown in Fig. 1.

"850" Trial

Progenies were allocated as follows:

- families within sets—three sets of 25 families and a fourth of 31 families
- sets within replications (four sets/rep)
- 10 replications per site
- non-contiguous plots of five trees/family individually randomised within each replication for sets 1 to 3, and an average of 3.5 trees for set 4.

The different geographic groups ("sources") of parent clones were sampled so as to give equal representation in the four sets.

"888" Trial

Progenies and controls were allocated as follows:

- families within sets (27–28 families + two to three controls/set)
- sets within replications (12 sets/replication)
- 32 replications per site
- one tree per family per replication

As shown in Table 2, the number of entries was different for different regional groups ("sources"). This resulted in having between one and two sets per region, and four sets contained entries from more than one region.

Field Assessments

The six locations of the "850" trial were assessed between November 1983 and February 1984, when the trial was about 8 1/2 years from planting. The three locations of the "888" trial were measured in January 1996 (Kaingaroa, age 6 1/2), December 1996 (Kinleith, age 7 1/2), and January 1998 (Pouto, age 8 1/2) respectively. Data for this report were taken from all nine locations. The assessment criteria used have been routinely used in the New Zealand *P. radiata* breeding programme since 1983 (Table 3). Branch cluster frequency score was assessed as a surrogate for counting branch clusters (Jayawickrama, Shelbourne & Carson 1997) while needle retention score was assessed primarily to rank entries for resistance to *Cyclaneusma minus* (Butin) DiCosmo *et al.* Acceptability was not assessed in the "850" polycross trial, nor needle retention at Berwick or Woodhill.

There are substantial regional differences in the expression of traits in New Zealand (Carson 1996). For a given seedlot, for example, there will be a high proportion of multinodal trees on Northland sands, a high proportion of long-internode trees in Southland, and a wide range of expression in the central North Island. Stem straightness is usually good on the Northland sands but quite variable in the central North Island. To discriminate better between genetic entries, the scoring is calibrated in an attempt to use the full range. This tends to affect the trees in the centre of the scale more than those at the extremes. A perfectly uninodal tree would be scored as 1 on any site, and a very multinodal tree would obtain a score of 9, but a tree scored as 5 on a Northland sand may be scored higher on a Southland site.

TABLE 3–Assessment criteria.

Traits	Assessment criteria
Diameter	In millimetres, at breast height (1.4 m)
Straightness	Subjective 1–9 scale (1 = very crooked , 9 = very straight)
Branch cluster frequency	Subjective 1–9 scale (1 = one branch cluster per year, 9 = several branch clusters per year)
Malformation	Subjective 1–9 scale (1 = multiple forking, 9 = no malformation)
Needle retention	Subjective 1–6 scale, where each complete year's foliage = 2
Acceptability	Acceptability = 1 if tree is subjectively judged likely to develop into an acceptable crop tree, = 0 if judged unacceptable

Statistical Analysis

We used the following linear model for statistical analyses of the "850" trial:

$$\text{Trait} = \text{mean} + \text{site} + \text{replication (site)} + \text{seed source} + \text{family(source)} + \text{site} \times \text{seed source} + \text{site} \times \text{family(source)} + \text{error} \quad (1)$$

where trait = diameter, straightness, etc. Since there were significant site × seed source interactions the data were also analysed by site, with the following linear model:

$$\text{Trait} = \text{mean} + \text{replication} + \text{seed source} + \text{family(source)} + \text{error} \quad (2)$$

We had previously run this test including the set effect, and found one significant set effect in 35 F-tests. Since one F-test in 20 is likely to give a p-value less than 0.05, even in the absence of a statistically significant treatment effect, we dropped sets from the model. In the "888" trial, sets could not be effectively separated from seed sources. The same models (equations 1 and 2) were therefore used, across and within sites. There were significant site × seed source interactions for this trial as well.

Analysis of variance was conducted using PROC GLM in SAS (SAS Institute Inc. 1990). Site, replication, set, and family were deemed random effects and hypothesis tests were obtained using the TEST option. Multiple comparison of seed sources was done with MEANS / TUKEY LINES options in PROC GLM. This provides a Tukey-Kramer test, which controls the maximum experimentwise error rate under any complete or partial null hypothesis and can be used with unequal sample sizes (Neter *et al.* 1990; SAS Institute Inc. 1990). Seed source means were also obtained from the MEANS option from PROC GLM described above.

Since the controls were not included in the ANOVA, their means were not obtained from PROC GLM but were calculated by site and then averaged across sites. For the seed sources we found the means resulting from this procedure to be almost identical to the means obtained from PROC GLM. No statistical comparisons were made between the controls and the seed sources, and the means are given for reference only.

Narrow-sense individual tree heritabilities were estimated at each site and across sites. The model used for the estimation of variance components had the same terms as used for the ANOVA (as shown in equations 1 and 2). Variance components were estimated using PROC VARCOMP Method = Type 1 (SAS Institute Inc. 1990). Heritabilities within sites were estimated as:

$$h^2 = 4\,\sigma^2_{family(source)} / \sigma^2_{family(source)} + \sigma^2_{error} \quad (3)$$

Heritabilities across sites were estimated as:

$$h^2 = 4\,\sigma^2_{family(source)} / \sigma^2_{family(source)} + \sigma^2_{site * family(source)} + \sigma^2_{error} \quad (4)$$

Standard errors for the heritabilities were estimated using the formula given by Becker (1992, p. 48).

RESULTS

Narrow-sense heritability estimates are given in Table 4. In general the heritabilities obtained were acceptably high in both series for diameter, straightness score, branch cluster frequency score, and needle retention score. For the "850" trial heritabilities were markedly higher at Kaingaroa for diameter, straightness score, branch cluster frequency score, and malformation score.

The only trait with significant seed-source effects across sites in the "850" trial was branch cluster frequency score (Table 5). There were significant site × seed source interactions, however, and significant seed-source effects for diameter, straightness score, branch cluster frequency score, and malformation score at Kaingaroa (Table 5). There were significant differences among seed sources for all traits in the "888" trial except malformation score at Pouto (Table 6).

Seed source means across sites for the "850" trial, means by site for the same, means across sites for "888" trial, and means by site for the same, are given in Tables 7, 8, 9, and 10 respectively. The highest branch cluster frequency score was for the Kaingaroa second-rotation selections, with almost a full point on the scale less for the Nelson source (Table 7). The Kaingaroa second-rotation group also had the highest diameter, straightness score, and

TABLE 4–Estimates of narrow-sense individual-tree heritabilities (h^2) and standard errors of the estimates (s.e.), for the "850" series polycross and the "888" series open-pollinated trials.

Series and site	Dbh		Straight-ness score		Branch cluster frequency score		Malfor-mation score		Needle retention score		Accep-table stems (%)	
	h^2	*s.e.*	h^2	*s.e.*	h^2	*s.e.*	h^2	*s.e.*	h^2	*s.e.*	h^2	*s.e.*
"850" polycross												
Woodhill	0.24	*0.05*	0.18	*0.04*	0.50	*0.07*	0.06	*0.03*	–		–	
Maramarua	0.07	*0.02*	0.14	*0.03*	0.26	*0.05*	0.05	*0.02*	0.12	*0.03*	–	
Kaingaroa	0.36	*0.05*	0.33	*0.05*	0.59	*0.07*	0.17	*0.03*	0.21	*0.04*	–	
Golden Downs	0.16	*0.04*	0.27	*0.05*	0.46	*0.06*	0.13	*0.03*	0.25	*0.05*	–	
Eyrewell	0.28	*0.05*	0.16	*0.04*	0.38	*0.06*	0.05	*0.02*	0.21	*0.04*	–	
Berwick	0.22	*0.04*	0.15	*0.04*	0.30	*0.05*	0.08	*0.03*	–		–	
Overall	0.10	*0.02*	0.15	*0.02*	0.31	*0.04*	0.03	*0.01*	0.09	*0.02*		
"888" open-pollinated												
Pouto	0.20	*0.02*	0.22	*0.03*	0.42	*0.04*	0.10	*0.02*	0.24	*0.03*	0.09	*0.02*
Kinleith	0.20	*0.03*	0.24	*0.03*	0.42	*0.04*	0.08	*0.02*	0.36	*0.04*	0.11	*0.02*
Kaingaroa	0.16	*0.02*	0.16	*0.02*	0.33	*0.03*	0.06	*0.02*	0.10	*0.02*	0.07	*0.02*
Overall	0.13	*0.02*	0.17	*0.02*	0.34	*0.03*	0.04	*0.01*	0.12	*0.02*	0.06	*0.02*

TABLE 5–F tests (ratios of mean squares) from mixed model analysis of variance for the "850" series polycross trial.

Source	Df	Dbh		Straightness		Branch cluster frequency		Needle retention		Malformation	
		Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value
Overall analysis											
Site	5	181.88	0.0001	0.67	0.6513	5.27	0.0005	31.19	0.0001	27.96	0.0001
Rep(Site)	54	46.79	0.0001	37.63	0.0001	40.96	0.0001	115.31	0.0001	9.43	0.0001
Seed source	5	1.00	0.4243	1.93	0.0970	5.29	0.0002	0.51	0.7665	1.38	0.2513
Fam(Seed source)	103	3.41	0.0001	6.07	0.0001	10.68	0.0001	2.50	0.0001	1.77	0.0001
Site*Seed source	25	1.83	0.0099	1.28	0.1742	1.68	0.0233	1.95	0.0198	1.38	0.1104
Rep(Site)*Seed source	270	1.01	0.4403	1.08	0.1773	1.29	0.0009	1.11	0.1573	0.91	0.8457
Site*Fam(Seed source)	481	2.14	0.0001	1.49	0.0001	1.69	0.0001	2.25	0.0001	1.58	0.0001
Error	21 708										
Total	22 651										
Site = Berwick											
Rep	9	59.09	0.0001	12.05	0.0001	52.13	0.0001			7.84	0.0001
Seed source	5	0.86	0.5140	1.72	0.1414	4.16	0.0020			0.47	0.7955
Fam(Seed source)	94	2.59	0.0001	2.10	0.0001	3.00	0.0001			1.64	0.0001
Seed source*rep	45	1.30	0.0875	1.06	0.3715	1.25	0.1270			1.05	0.3795
Error	3 066										
Site = Eyrewell											
Rep	9	14.45	0.0001	21.46	0.0001	53.00	0.0001	263.29	0.0001	5.14	0.0001
Seed source	5	0.89	0.4896	0.46	0.8066	3.27	0.0088	1.50	0.1993	0.73	0.6053
Fam(Seed source)	95	4.82	0.0001	2.91	0.0001	4.94	0.0001	3.33	0.0001	1.62	0.0002
Seed source*rep	45	1.40	0.0416	1.32	0.0767	1.77	0.0012	0.96	0.5554	0.79	0.8392
Error	4 117										

Note: ANOVA model run on SAS / PROC GLM with seed source as a fixed effect and all others as random effects.

TABLE 5–cont.

Source	Df	Dbh		Straightness		Branch cluster frequency		Needle retention		Malformation	
		Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value
Site = Golden Downs											
Rep	9	180.87	0.0001	117.78	0.0001	57.06	0.0001	5.04	0.0001	7.92	0.0001
Seed source	5	1.14	0.3481	1.57	0.1777	5.71	0.0001	0.80	0.5496	0.80	0.5569
Fam(Seed source)	99	2.84	0.0001	3.19	0.0001	4.02	0.0001	3.13	0.0001	1.96	0.0001
Seed source*rep	45	1.04	0.3998	0.89	0.6741	1.10	0.2981	1.01	0.4471	0.90	0.6668
Error	3277										
Site = Kaingaroa											
Rep	9	3.72	0.0009	41.01	0.0001	11.15	0.0001	194.94	0.0001	9.17	0.0001
Seed source	5	2.86	0.0191	2.66	0.0274	4.75	0.0006	2.06	0.0775	2.42	0.0425
Fam(Seed source)	100	4.97	0.0001	4.35	0.0001	7.34	0.0001	3.54	0.0001	2.56	0.0001
Seed source*rep	45	0.88	0.6924	0.97	0.5232	1.14	0.2364	1.15	0.2315	1.03	0.4199
Error	4463										
Site = Maramarua											
Rep	9	44.48	0.0001	22.60	0.0001	31.74	0.0001	49.51	0.0001	14.14	0.0001
Seed source	5	1.43	0.2288	2.10	0.0748	3.50	0.0060	0.77	0.5757	2.23	0.0668
Fam(Seed source)	101	1.60	0.0002	2.28	0.0001	3.43	0.0001	2.44	0.0001	1.41	0.0052
Seed source*rep	45	0.80	0.8288	1.23	0.1421	1.53	0.0134	1.28	0.0976	0.78	0.8586
Error	3696										
Site = Woodhill											
Rep	9	14.68	0.0001	47.33	0.0001	49.81	0.0001			15.16	0.0001
Seed source	5	0.92	0.4748	0.98	0.4326	2.78	0.0220			0.82	0.5405
Fam(Seed source)	95	2.96	0.0001	2.67	0.0001	5.19	0.0001			1.56	0.0005
Seed source*rep	45	1.12	0.2756	1.05	0.3841	1.20	0.1724			0.95	0.5740
Error	3089										

Note: ANOVA model run on SAS / PROC GLM with seed source as a fixed effect and all others as random effects.

TABLE 6–F tests (ratios of mean squares) from mixed model analysis of variance for the "888" series open-pollinated trial.

Source	Df	Dbh		Straightness		Branch cluster frequency		Malformation		Needle retention		Acceptability	
		Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value	Ratio	P-value
Overall													
Site	2	195.62	0.0001	159.04	0.0001	339.20	0.0001	361.67	0.0001	137.57	0.0001	283.13	0.0001
Rep(Site)	93	18.95	0.0001	16.88	0.0001	14.15	0.0001	4.07	0.0001	48.37	0.0001	6.25	0.0001
Seed source	6	7.01	0.0001	7.38	0.0001	6.09	0.0001	3.51	0.0023	3.67	0.0001	7.71	0.0001
Family(Seed source)	311	3.04	0.0001	3.88	0.0001	6.74	0.0001	1.63	0.0001	2.37	0.0001	2.09	0.0001
Site*Seed source	12	4.67	0.0001	2.96	0.0005	2.83	0.0008	1.16	0.3059	2.70	0.0015	2.73	0.0013
Site*Family(Seed source)	622	1.45	0.0001	1.31	0.0001	1.40	0.0001	1.33	0.0001	1.92	0.0001	1.22	0.0002
Error	26 298												
Site = Pouto													
Rep	31	17.66	0.0001	6.13	0.0001	18.08	0.0001	1.79	0.0046	28.05	0.0001	10.98	0.0001
Seed source	6	5.87	0.0001	4.74	0.0001	4.74	0.0001	0.50	0.8064	2.33	0.0325	2.97	0.0079
Family(source)	311	2.66	0.0001	2.86	0.0001	4.64	0.0001	1.79	0.0001	2.98	0.0001	1.72	0.0001
Error	9 591												
Site = Kinleith													
Rep	31	18.91	0.0001	20.77	0.0001	15.82	0.0001	3.79	0.0001	68.30	0.0001	4.59	0.0001
Seed source	6	6.03	0.0001	5.87	0.0001	6.02	0.0001	2.23	0.0405	2.26	0.0377	4.25	0.0004
Family(source)	311	2.50	0.0001	2.78	0.0001	4.28	0.0001	1.60	0.0001	3.77	0.0001	1.77	0.0001
Error	8 601												
Site = Kaingaroa													
Rep	31	19.36	0.0001	21.48	0.0001	8.74	0.0001	5.50	0.0001	39.64	0.0001	3.82	0.0001
Seed source	6	6.29	0.0001	6.87	0.0001	5.17	0.0001	3.20	0.0046	5.92	0.0001	8.14	0.0001
Family(source)	311	2.12	0.0001	2.09	0.0001	3.39	0.0001	1.42	0.0001	1.69	0.0001	1.48	0.0001
Error	8 106												

Note: ANOVA model run on PROC GLM with seed source as a fixed effect and other terms as random effects.

TABLE 7–Seed source means across sites for the "850" series polycross trial.

Seed source	Number of trees measured	Dbh	Straightness score	Branch cluster frequency score	Malformation score	Needle retention score
Kaingaroa (second rotation)	1593	164 a	6.29 a	5.81 a	7.92 a	4.67 a
Kaingaroa (old crop)	3536	163 ab	5.93 bc	5.60 b	7.71 b	4.63 ab
Kinleith (old crop)	3396	161 bc	6.00 b	5.45 c	7.74 b	4.63 ab
Nelson	4049	161 bc	5.76 d	4.86 f	7.65 b	4.64 ab
Canterbury	4715	160 c	5.84 cd	5.17 d	7.62 b	4.59 b
Southland	5363	161 bc	5.88 bcd	5.02 e	7.65 b	4.63 ab
"850" Gwavas orchard*	976	158	5.90	5.38	7.69	4.64
Unimproved Kaingaroa bulk*	936	152	5.24	4.55	7.56	4.53

* Controls were not involved in the analysis of variance, and their means are included for comparison only.

Note: Seed source means followed by the same letter (a, b, c, d, e, or f) were not significantly different from each other, according to a Tukey-Kramer multiple comparison test.

malformation score at Kaingaroa, the only site with significant seed-source differences for these traits (Table 8); there its branch cluster frequency score was a full 1.5 points higher than that of the Nelson seed source. The Kaingaroa second-rotation group was the straightest at the other five sites as well, and had the least malformation on four of these five sites. This group outperformed the open-pollinated "850" orchard lot for diameter, straightness, and malformation and had a higher branch cluster frequency score. At Berwick the Southland source had the highest diameter and ranked second for straightness and malformation. The unimproved Kaingaroa bulk seedlot had the lowest diameter, branch cluster frequency, malformation score, and needle retention across sites (Table 7).

For the "888" trial, the Tarawera seed source had the highest branch cluster frequency score, needle retention score, malformation score, and percentage of acceptable stems (Table 9). This source was intermediate between the "850" and "268" open-pollinated orchard seedlots for diameter, straightness score, malformation score, and percentage of acceptable stems. The Southland and Nelson sources had the lowest diameter (by a few millimetres), while the Southland source had noticeably lower branch cluster frequency (Table 9). The poorest straightness and malformation scores and acceptabilities were for the Northland and Tahorakuri sources, and their means were comparable with the Kaingaroa climbing select seedlot (Table 9). The Tahorakuri source had the highest diameter by a narrow margin, while the Chilean source was intermediate for all the traits assessed. The "268" Kaingaroa orchard seedlot had the highest straightness, branch cluster frequency, and acceptability scores (Table 9).

The separation between the sources with the highest and the lowest values was slightly higher for the "850" trial than for the "888" trial, for branch cluster frequency score (0.95 *v.* 0.62) and for straightness score (0.53 *v.* 0.41). The reverse was true for diameter, by a small margin (6 mm *v.* 4 mm).

TABLE 8–Seed source means, by site, for the "850" series polycross trial.

Seed source	Number of trees measured	Dbh (mm)	Straight-ness score	Branch cluster frequency score	Malfor-mation score	Needle retention score
Site = Berwick						
Kaingaroa (second rotation)	223	112 a	6.15 a	5.42 a	8.03 a	
Kaingaroa (old crop)	479	114 a	5.61 b	5.19 a	7.79 a	
Kinleith (old crop)	521	115 a	5.75 b	5.17 a	7.98 a	
Canterbury	652	114 a	5.73 b	4.54 b	7.94 a	
Nelson	578	115 a	5.57 b	4.72 b	7.87 a	
Southland	767	116 a	5.81ab	4.65 b	8.00 a	
Site = Eyrewell						
Kaingaroa (second rotation)	281	124 a	6.23 a	6.15 ab	8.25 a	5.91 ab
Kaingaroa (old crop)	641	121 ab	6.03 a	6.36 a	8.05 a	5.89 ab
Kinleith (old crop)	706	124 a	6.20 a	6.14 ab	7.96 a	5.79 b
Canterbury	883	123 ab	6.03 a	5.98 bc	7.98 a	5.95 a
Nelson	776	122 ab	5.99 a	5.64 d	8.06 a	5.99 a
Southland	985	122 ab	6.08 a	5.72 dc	7.99 a	5.90 ab
Site = Golden Downs						
Kaingaroa (second rotation)	240	144 a	6.60 a	6.03 a	7.98 a	4.76 a
Kaingaroa (old crop)	539	147 a	6.17 b	5.51 b	8.02 a	4.73 a
Kinleith (old crop)	483	146 a	6.27 b	5.16 bc	7.81 a	4.78 a
Canterbury	739	144 a	5.97 c	5.00 c	7.76 a	4.63 a
Nelson	590	143 a	5.99 bc	4.57 d	7.77 a	4.72 a
Southland	845	145 a	6.03 bc	4.87 cd	7.84 a	4.69 a
Site = Kaingaroa						
Kaingaroa (second rotation)	322	236 a	6.31 a	5.44 a	7.18 a	3.95 a
Kaingaroa (old crop)	734	232 ab	5.89 b	5.02 b	6.65 bc	3.90 ab
Kinleith (old crop)	662	229 bc	5.92 b	4.73 b	6.95 ab	3.76 bc
Canterbury	988	224 d	5.54 cd	4.31 c	6.47 c	3.74 c
Nelson	808	225 cd	5.44 d	3.94 d	6.41 c	3.71 c
Southland	1109	229 bc	5.76 bc	4.23 cd	6.63 bc	3.84 abc
Site = Maramarua						
Kaingaroa (second rotation)	304	155 a	6.29 a	5.99 a	8.37 a	4.21 a
Kaingaroa (old crop)	617	150 ab	5.81 b	5.76 ab	8.27 ab	4.09 ab
Kinleith (old crop)	532	152 ab	5.99 b	5.75 ab	8.29 ab	4.06 b
Canterbury	806	148 b	5.98 b	5.64 bc	8.17 ab	4.11 ab
Nelson	689	150 ab	5.77 b	5.18 d	8.22 ab	4.13 ab
Southland	909	150 ab	5.83 b	5.44 cd	8.10 b	4.16 ab
Site = Woodhill						
Kaingaroa (second rotation)	223	191 ab	6.11 a	5.83 a	7.80 a	
Kaingaroa (old crop)	526	193 ab	6.05 ab	5.77 a	7.71 a	
Kinleith (old crop)	492	195 ab	5.86 ab	5.70 a	7.60 a	
Canterbury	647	193 ab	5.81 ab	5.61 a	7.69 a	
Nelson	608	196 a	5.82 ab	5.15 b	7.77 a	
Southland	748	190 b	5.73 b	5.28 b	7.60 a	

Note: Seed source means followed by the same letter (a, b, c, or d) were not significantly different from each other according to a Tukey-Kramer multiple comparison test.

TABLE 9–Seed source means across sites for the "888" series trial.

Seed source	Number of trees measured	Dbh	Straight-ness score	Branch cluster frequency score	Malfor-mation score	Needle retention score	Accep-table stems (%)
Tarawera	3730	192 ab	5.52 a	5.33 a	7.11 a	3.67 a	54 a
Hawke's Bay	4744	190 c	5.56 a	5.06 b	6.96 ab	3.60 bc	53 a
Nelson	4180	186 d	5.51 a	4.92 c	6.94 b	3.59 bc	52 ab
Northland	4221	191 bc	5.20 c	5.02 bc	6.83 bc	3.62 abc	46 d
Southland	4253	187 d	5.34 b	4.71 d	6.93 b	3.50 d	49 bc
Tahorakuri	2417	193 a	5.15 c	4.91 c	6.74 c	3.64 ab	46 cd
Chile	3800	190 c	5.50 a	5.21 a	6.90 bc	3.56 c	52 ab
"268" Kaingaroa orchard*	887	193	6.02	6.08	7.41	3.64	62
"850" Gwavas orchard*	847	189	5.27	5.42	7.02	3.60	48
Kaingaroa climbing select*	750	185	5.16	4.85	6.86	3.55	45

* Controls were not involved in the Analysis of Variance, and their means are included for comparison only.

Note: Seed source means followed by the same letter (a, b, c, or d) were not significantly different from each other according to a Tukey-Kramer multiple comparison test.

DISCUSSION AND CONCLUSIONS

Overall Trends

The overall trend from both these studies was for a higher branch cluster frequency score, less malformation, and good straightness for progeny of selections made in second-rotation stands in the central North Island. Sources from Nelson and Southland had lower branch cluster frequency scores in both trials. As a point of reference, a perfectly uninodal tree (branch cluster frequency score = 1) could have one branch cluster per year and an internode length of 2 m on a good site, while an extremely multinodal tree (score = 9) could have six clusters per year and an internode length of 35 cm (Jayawickrama, Shelbourne & Carson 1997). The best performance of the Southland source was on a Southland site (Berwick). Based on these and other data, seed from an "850" series "Southland" clonal orchard were thought to give reasonable genetic gain when planted in the Southland region but were clearly outperformed by the central North Island "850" orchard elsewhere in the country (Shelbourne *et al.* 1986; Forest Research Institute 1987). The same applied to a "Canterbury" orchard (Vincent 1993).

In both trials, the group of selections from second-rotation sites in the central North Island had better straightness and malformation scores and higher dbh than the "850" Gwavas seedlot. In the "850" trial, the Kaingaroa second-rotation source was tested as polycross progenies, which could given them an advantage over open-pollinated seed. The genetic quality of open-pollinated orchard seed is reduced by contamination from non-orchard pollen. In contrast, none of the sources was superior to the "268" Kaingaroa orchard seedlot; this was as expected, given that the seedlot came from a rogued orchard entering maturity.

TABLE 10–Seed source means, by site, for the "888" series trial.

Seed source	Number of trees measured	Dbh	Straightness score	Branch cluster frequency score	Malformation score	Needle retention score	Acceptable stems (%)
Site = Pouto							
Tarawera	1347	192 a	6.47 ab	6.51ab	8.10 a	3.31 bc	0.75 ab
Hawke's Bay	1722	191 a	6.52 a	6.40 bc	7.99 a	3.31 bc	0.75 ab
Nelson	1531	186 b	6.34 bc	6.26 cd	7.94 a	3.24 c	0.70 bc
Northland	1543	192 a	6.20 c	6.22 cde	7.96 a	3.35 ab	0.70 c
Southland	1537	188 b	6.22 c	6.05 e	8.01 a	3.26 c	0.69 c
Tahorakuri	871	191 a	6.21 c	6.17 de	7.99 a	3.40 a	0.71 abc
Chile	1389	193 a	6.54 a	6.63 a	8.02 a	3.26 c	0.75 a
Site = Kinleith							
Tarawera	1235	208 b	5.13 a	4.98 a	6.22 a	4.52 ab	0.39 a
Hawke's Bay	1557	208 b	5.15 a	4.67 bc	6.12 ab	4.48 ab	0.36 ab
Nelson	1375	203 c	5.12 ab	4.50 c	6.04 abc	4.49 ab	0.36 ab
Northland	1374	206 bc	4.75 cd	4.69 b	5.86 bc	4.51 ab	0.29 c
Southland	1406	206 bc	4.93 bc	4.20 d	5.98 abc	4.33 c	0.33 bc
Tahorakuri	784	213 a	4.63 d	4.61 bc	5.75 c	4.56 a	0.29 c
Chile	1219	204 c	4.92 c	4.79 ab	5.93 abc	4.44 b	0.32 bc
Site = Kaingaroa							
Tarawera	1148	176 a	4.82 ab	4.31 a	6.91 a	3.18 a	0.47 a
Hawke's Bay	1465	171 bc	4.87 ab	3.90 bc	6.64 abc	3.01 b	0.45 a
Nelson	1274	168 cd	4.95 a	3.79 bcd	6.71 ab	3.03 b	0.47 a
Northland	1304	173 ab	4.47 c	3.95 bc	6.50 bc	2.99 bc	0.35 b
Southland	1310	167 d	4.74 b	3.67 d	6.68 ab	2.89 c	0.42 a
Tahorakuri	762	173 ab	4.47 c	3.76 cd	6.33 c	2.95 bc	0.36 b
Chile	1192	172 bc	4.89 ab	3.99 b	6.58 abc	3.01 b	0.44 a

Note: Seed source means followed by the same letter (a, b, c, d, or e) were not significantly different from each other according to a Tukey-Kramer multiple comparison test.

"888" Trial

The Tahorakuri source did have a marginally higher diameter than the others in the "888" trial. However, if the parent trees were indeed the survivors of very heavy regeneration (as many as 400 000 seedlings/ha) the selection rate of the plus-trees could be as high as 1 per 700 000 seedlings regenerated (28 trees were selected in 50 ha). The stands were very dense for several years. For such intense selection for competitive ability the results were disappointing. It is reported that selective logging took place in this stand several years before the plus-tree selection, removing the best trees for peeler logs; perhaps some of the best genotypes were removed this way.

The Chilean source showed good growth and form (Table 9) and was comparable to the "850" Gwavas orchard seedlot. The performance of these progenies in New Zealand was good, given that the orchard was unrogued at the time and given that the parents had not been selected under New Zealand conditions.

Reasons for the Significant Seed-source Effects

We propose several reasons for the expression of significant seed source effects.

Better selection of plus-trees in some forests

The environmental conditions in some forests (e.g., Kaingaroa second-rotation and Tarawera) may allow trees to express their genetic potential better, and make selection of plus-trees more effective. In other words, it can be hypothesised that a tree with the genetic potential to grow crooked would be more crooked on these sites, whereas a tree with the same potential but growing on a Northland sand site would be more likely to grow straight. The average straightness at Pouto was 6.4 but only 4.8 at Kaingaroa for the "888" series. This is a reflection of the better straightness on such sites, and occurred despite the effort described previously to calibrate the scoring to obtain a wide range (and good discrimination of families) at each site.

Founder effects

Significant founder effects may have occurred, resulting from different regions having a preponderance of planting stock derived from different native populations. Burdon (1992a) and others (Burdon *et al.* 1992; Burdon, Broekhuizen & Zabkiewicz 1997) found evidence that the Nelson land race had more affinity to the Monterey native population than had the Kaingaroa land race.

Natural selection

Different natural selection pressures may be exerted in different parts of the country, such as a possible selective advantage for descendants of the Monterey provenance on the more infertile soils of the Nelson region (Burdon, Broekhuizen & Zabkiewicz 1997).

Discrimination against long internode trees

Low branch cluster frequency (the long internode habit) is more common in Southland and the Nelson region (Carson & Inglis 1988). Internode length has adverse genetic correlations with diameter growth, straightness, and malformation score (Jayawickrama, Shelbourne & Carson 1997). In the central North Island, selecting big well-formed plus-trees tends to discriminate against long internode trees. However, in stands where the long internode habit is more frequent, the discrimination may be less. Selection against stem cones low in the stem could also favour long-internode trees, since such trees tended to produce cones later and therefore higher on the stem (J.T.Miller pers. comm.). These could explain why the Southland and Nelson sources had lower branch cluster frequency scores in both trials. The Southland "land race" had lower branch cluster frequency than the Kaingaroa "land race" in a third, independent trial (Burdon, Firth, Low & Miller 1997).

Artificial selection

The "850" series included selections from stands planted from 1889 through to 1954 (Table 1). The later stands could have benefited from an extra cycle of silvicultural selection compared to the earlier stands, enhancing the seed source differences. The "888" plus-trees were selected in plantations with a narrower range of establishment dates (1947–74 ; Table 2). The Tarawera plus-trees in the "888" trial were selected in one of the early plantations established with "climbing select" planting stock, equivalent to seed trees as referred to by Zobel & Talbert (1984). In other words, these stands already had some genetic improvement in addition to natural / silvicultural selection.

Comparison of the Two Trials

The resolution of seed source differences was sharper in the "888" series trial than in the "850" polycross trial (cf. Table 6 and Table 5). This could have arisen from the fact that all polycross progenies in the "850" trial had the same pollen parents, while the open-pollinated progenies within a seed source of the "888" trial originated from pollen of the same seed source. Another possible reason is that the current subjective assessment scale was used for the first time in the "850" polycross trial in 1983, but was a very routine procedure by the time the "888" series was assessed. A third difference between the two trials was that one team of field personnel selected all the plus-trees for the "888" series (not the case for the "850" series), and the selection was completed in a year as against 17 years for the "850" series. The "850" trial was also planted over a much wider latitudinal distribution than the "888" trial, with the potential for greater genotype × environment interaction.

Implications of the Results for Breeding and Deployment

The differences among the seed sources, although capable of affecting the profitability of growing plantations, were smaller than the differences seen among the provenances of this species in common-garden trials in New Zealand (Burdon *et al.* 1992). We traced the Nelson source in the "888" series trial back two (in some cases three) generations in the Nelson region. However, as mentioned previously, there is evidence for movement of seed across regions. Further, since the species was planted in this country only since the mid-nineteenth century, not enough time appears to have passed to allow large genetic differences between plantations in different regions. Now that planting is almost exclusively with seed orchard material, such spontaneous differentiation is unlikely to go further.

The good performance of the Kaingaroa second-rotation and Tarawera sources is important, given that the two largest plus-tree selection efforts in the New Zealand breeding programme (the "268" series in 1968 and the "885" series in 1985) were in the Northern Boundary area of Kaingaroa Forest, in plantations established between 1951 and 1968. For the "268" selection, the decision to select in this area was due mainly to having a sizable plantation base of the age deemed best suited for plus-tree selection.

The current understanding is that the progeny of genotypes well ranked on three or four sites (including a central North Island site) can be expected to grow well on almost any representative plantation site in New Zealand. Top-ranked production parents are successfully used for reforestation in Australia as well. The good performance of the Chilean progenies in New Zealand is consistent with these results and with the plasticity and wide adaptability of this species.

The early selection of long-internode plus-trees was in the central North Island. Given the propensity of the Southland and Nelson sources to have long internodes, we can speculate if using them as a starting point would have made a difference. Be that as it may, some of the Southland and Nelson selections could be used if there was interest in increasing internode length, as for the long internode breed (Jayawickrama, Shelbourne & Carson 1997).

ACKNOWLEDGMENTS

C.J.A.Shelbourne masterminded the "850" polycross trial, A.Firth and J.T.Miller were responsible for the controlled pollinations and T.G.Vincent for the trial establishment. R.D.Burdon, R.L.Cameron,

M.Cochrane, A.Firth, C.B.Low, M.Miller, C.J.A.Shelbourne, G.Stovold, and N.Woods measured the trees at age 8. Sites for this trial were provided by the New Zealand Forest Service.

The "888" series progeny tests were established by R.Johnson, C.B.Low, M.Miller, W.Brown, T.G.Vincent, R.McConnochie, and G.Stovold. R.L.Cameron, M.Miller, R.Parr, and J.Wharekura measured the trees at age 8. The sites for this trial were made available by NZ Timberlands Ltd, Tasman Forestry Ltd, and NZ Forest Products Ltd. Other staff members of the Genetics and Tree Improvement section at the New Zealand Forest Research Institute have contributed to both these trials in various ways. Funding for measurement and data analyses was provided by the New Zealand Radiata Pine Breeding Co-operative and the New Zealand Government, first through the New Zealand Forest Service and later through the Foundation for Research, Science and Technology. R.D.Burdon, S.E.McKeand, A.C.Matheson, and C.J.A.Shelbourne made valuable suggestions on earlier versions of this paper.

REFERENCES

BECKER, W.A. 1992: "Manual of Quantitative Genetics", fifth edition. Academic Enterprises, Pullman, WA, USA.

BURDON, R.D. 1992a: Genetic survey of *Pinus radiata*. 9: General discussion and implications for genetic management. *New Zealand Journal of Forestry Science 22(2/3)*: 274–298.

———1992b: Introduced forest trees in New Zealand: Recognition, role and seed source. 12. Radiata pine (*Pinus radiata* D. Don). J.T.Miller (Ed.). *New Zealand Forest Research Institute, FRI Bulletin No. 124.*

BURDON, R.D.; BANNISTER, M.H.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 2: Population comparisons for growth rate, disease resistance, and morphology. *New Zealand Journal of Forestry Science 22(2/3)*: 138–159.

BURDON, R.D.; BROEKHUIZEN, P.; ZABKIEWICZ, J.A. 1997: Comparison of native-population and New Zealand land-race samples of *Pinus radiata* using cortical oleoresin monoterpenes. Pp. 50–56 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO'97 Genetics of Radiata Pine", Proceedings of NZFRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. *New Zealand Forest Research Institute, FRI Bulletin 203.*

BURDON, R.D.; FIRTH, A.; LOW, C.B.; MILLER, M.A. 1997: Native provenances of *Pinus radiata* in New Zealand: Performance and potential. *New Zealand Forestry 41(4)*: 32–36.

CARSON, M.J.; INGLIS, C.S. 1988: Genotype and location effects on internode length of *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* 18(3): 267–279.

CARSON, S.D. 1996: Greater specialisation of improved seedlots in New Zealand: New developments for efficient selection of parents and evaluation of performance. *New Zealand Forestry 41(1)*: 12–17.

FALKENHAGEN, E.R. 1991: Provenance variation in *Pinus radiata* at six sites in South Africa. *Silvae Genetica 40*: 41–50.

FOREST RESEARCH INSTITUTE 1987: Which radiata pine seed should you use? *New Zealand Ministry of Forestry, What's New in Forest Research No. 157.*

JAYAWICKRAMA, K.J.S.; BALOCCHI, C. 1993: Growth and form of provenances of *Pinus radiata* in Chile. *Australian Forestry 56(2)*: 172–178.

JAYAWICKRAMA, K.J.S.; SHELBOURNE, C.J.A.; CARSON, M.J. 1997: New Zealand's long internode breed of *Pinus radiata*. *New Zealand Journal of Forestry Science* 27(2): 126–141.

JAYAWICKRAMA, K.J.S.; CARSON, M.J.; JEFFERSON, P.A.; FIRTH, A. 1997: Development of the New Zealand radiata pine breeding population. Pp. 217–225 *in* Burdon, R.D.; Moore, J.M. (Ed.) "IUFRO '97 Genetics of Radiata Pine". Proceedings of NZFRI-IUFRO Conference 1–4 December and Workshop 5 December, Rotorua, New Zealand. *New Zealand Forest Research Institute, FRI Bulletin No. 203.*

MacARTHUR, R.S. 1952: Early thinning treatment & growth development in stands of *Pinus radiata* D. Don. established at excessively high initial density. *New Zealand Journal of Forestry 6(4)*: 333–338.

MORGENSTERN, E.K. 1996: "Geographic Variation in Forest Trees". UBC Press, Vancouver, BC, Canada.

N. C. STATE UNIVERSITY 1994: Thirty-eighth annual report of the North Carolina State University - Industry Cooperative Tree Improvement Program. N.C.State University, Raleigh, NC, USA.

NETER, J.; WASSERMAN, W.; KUTNER, M.H. 1990: "Applied Linear Statistical Models". Third edition. Irwin, Homewood, IL, USA.

SAS INSTITUTE INC. 1990: "SAS/STAT User's Guide, Version 6". Fourth edition. SAS Institute Inc., Cary, NC, USA.

SCHUTZ, W.M.; COCKERHAM, C.C. 1966: The effects of field blocking on gain from selection. *Biometrics 22(4)*: 843–863.

SHELBOURNE, C.J.A.; BURDON, R.D.; CARSON, S.D.; FIRTH, A.; VINCENT, T.G. 1986: "Development Plan for Radiata Pine Breeding". New Zealand Forest Service, Forest Research Institute, Rotorua, New Zealand.

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. *Horticulture in New Zealand 1(1)*: 33–38.

SHEPHERD, W.; COOK, W. 1988: "The Botanic Garden Wellington: A New Zealand history 1840–1987". Millwood Press, Wellington, NZ.

VINCENT, T.G. 1993: Supply of improved radiata pine seed. *New Zealand Forestry 38(3)*: 45–48.

VINCENT, T.G.; DUNSTAN, J.S. 1989: Register of commercial seedlots issued by the New Zealand Forest Service. *New Zealand Ministry of Forestry, Forest Research Institute, FRI Bulletin No. 144.*

ZOBEL, B.; TALBERT, J. 1984: "Applied Forest Tree Improvement". John Wiley & Sons, New York.

ZOBEL, B.J.; VAN WYK, G.; STAHL, P. 1987: "Growing Exotic Forests". John Wiley & Sons, New York.

APPENDIX 1

The Sets-in-Replications design is a variant of the Randomised Complete Block Design and has been used in the New Zealand *Pinus radiata* breeding programme since 1969, first with row-plots and eventually with single-tree plots. In this design, entries were grouped into sets (typically 30–42 entries for progeny testing of *P. radiata*); aggregation of a number of sets (up to 16 for progeny testing) made up the replication. The Sets-in-Replications design was adopted for trials with many entries (up to 590) for the following reasons (C.J.A.Shelbourne & F.R.M.Cockrem unpubl. data):

- Replications would be large in such trials, with high within-replication environmental variation. It was expected that variation within a set would be less.
- Computing capabilities at the time could not handle large matrices, which had to be manipulated if analysing by replication. Trials could instead be analysed by set and the information pooled.
- Grouping entries into sets facilitated trial establishment.
- Balanced or partially unbalanced incomplete block designs were felt to have limitations in the number of entries accommodated, and to be difficult to establish and analyse.

APPENDIX 2

A. DESCRIPTION OF SITES* IN THE "850" SERIES POLYCROSS PROGENY TRIAL.

Site	Soil	Elev-ation (m)	Lat. (°S)	Site description and previous vegetation	Trees measured as percentage of trees planted	Comments
Woodhill Cpt 225, 230, and 231	Coastal sand, low in fertility	20	36°20′	Marram grass and lupin. Rows crushed by dozer before planting	66.3	Moderate survival.
Maramarua Cpt 29	Heavy clay	110	37°19′	*Pinus nigra* stand clearfelled to waste 1974–75, burned 1975.	79.2	Variable tree growth and heavy weed cover. Super-phosphate applied at 1 tonne/ha.
Kaingaroa Cpt 327	Volcanic ash and pumice	560	38°41′	Manuka, scattered Douglas fir and *P. radiata.* Crushed and burned in 1975.	94.7	Excellent survival. No weed or growth problems.
Golden Downs Cpt 345	Moutere gravel	670	41°35′	Grazing land. Moderately heavy bracken cover burnt in 1975.	71.2	Moderate survival.
Eyrewell Cpt 32	Stony silt loam, shallow rooting	180	43°25′	*P. radiata* stand windthrown in 1965. Deep ripped at 4 m spacing in 1975.	87.0	Suffered toppling in 1980 due to a gale.
Berwick Cpt 123	Yellow-brown earth	400	45°58′	Grazing land in short tussock grass. Ripped in May 1975, trees planted in ripped lines.	65.6	Cold, windy site, some waterlogging and snow damage.

* All six trials were planted at 4 × 4 m and occupied 9.2 ha each.

B. DESCRIPTION OF SITES* IN THE "888" SERIES PROGENY TRIAL.

Site	Soil	Elev-ation (m)	Lat. (°S)	Site description and previous vegetation	Trees measured as percentage of trees planted	Comments
Pouto A Cpt 17	Coastal yellow-brown sand.	30	36°20′	Marram grass and crushed lupin.	98	A successful trial with excellent survival and good uniformity.
Kinleith Cpt 6234	Yellow-brown pumice overlaid by organic topsoil.	380	38°16′	*Pinus radiata* plantation, V-bladed prior to planting.	88	Successful trial, but heavy incidence of blackberry. A flat site, located adjacent to the effluent ditch from the Kinleith pulp mill.
Kaingaroa Cpt 1269	Yellow-brown pumice overlaid by ash and gravelly ash.	400	38°20′	*Pinus radiata* plantation.	83	Rather variable in topography with notable ridges and depressions.

* The Pouto trial was planted at 3.5 × 3.5 m spacing and occupied 15.4 ha; the other two were planted at 4 × 4 m and occupied 18.4 ha.