

# GROWTH OF NATURAL CALIFORNIAN PROVENANCES OF *PINUS RADIATA* IN NEW SOUTH WALES, AUSTRALIA

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## ABSTRACT

Height and basal area data from a series of eight provenance trials of *Pinus radiata* D. Don planted in New South Wales were analysed at age 8 years. The trials tested subpopulations from the three mainland California natural populations—four from Año Nuevo, six from Monterey, and three from Cambria—as well as a single mixed-family seedlot from an Australian first-generation uncultured seed orchard. The test sites varied greatly in soil fertility and climate; mean tree height at age 8 years ranged from 4.7 to 11.2 m. There were significant differences in growth rate between populations on several sites, and overall there was a large population  $\times$  site interaction. Monterey was usually the best of the natural populations, but Año Nuevo grew better on the highest productivity sites and Cambria grew well on some low productivity sites. Despite the interaction, the seed orchard seedlot was the best population for growth at all sites. There was no evidence of subpopulation-within-population  $\times$  site interaction and, in contrast to several previous studies, there were significant differences between subpopulations within some populations.

**Keywords:** provenance; genotype  $\times$  site interaction; land race; tree breeding; *Pinus radiata*.

## INTRODUCTION

*Pinus radiata* is the most widely planted conifer in the Southern Hemisphere, and in the temperate zone of Australia it is by far the most important crop planted for wood production. The current area established with the species throughout the world is about 3.85 million ha

(Lavery & Mead in press). Despite its pre-eminent commercial importance and the general recognition that provenance testing should be one of the first steps in a domestication and breeding programme, comprehensive provenance testing of *P. radiata* was not commenced in Australia until the late 1970s, 20 years after intensive breeding began. Apparently, as *P. radiata* had such a restricted natural distribution (about 7000 ha), foresters and tree breeders considered until the early 1970s that there was little geographic variation in the species, and that existing variation had already been captured adequately in the local plantations which were the base populations for breeding.

The potential value to the genetic improvement of *P. radiata* of importing samples of wild populations did not go unrecognised, however. Bannister (1959) advocated extensive collections of seed from the natural stands, to enable breeders to incorporate greater genetic diversity into stock already selected from New Zealand sources. A genetic survey experiment with 50 open-pollinated progenies from each of the five natural populations was planted over four sites in New Zealand, between 1964 and 1967 (Burdon & Bannister 1973; Shelbourne *et al.* 1979; Burdon *et al.* 1997). In Australia, several small block plantings and trials with unreplicated plots were established in the 1940s and 1950s using seed from the five natural populations. These have been described briefly by Eldridge (1983). Two small replicated trials were established in Tallaganda State Forest, N.S.W., in 1969 and 1970, with seed from the range-wide collection made by Dr W. J. Libby. Some hybrid seedlots from Cambria, Guadalupe, and Cedros trees pollinated by local Australian or New Zealand stock, as well as natural Año Nuevo and Cambria progenies, were included in the large International Gene Pool trial established over a number of sites in 1972–73 at the instigation of Dr C. J. A. Shelbourne of the New Zealand Forest Research Institute. None of the Australian plantings before 1979 was adequate for investigating the potential of the natural populations to contribute to breeding populations, because of limitations in the numbers of parents or populations sampled, or the inadequacy of experimental designs or the range of sites over which they were planted.

More systematic attempts to assess the growth performance of *P. radiata* provenances occurred after a comprehensive seed collection was undertaken in the five natural populations in 1978 (Eldridge 1978, and unpubl. data; A. Firth unpubl. data). A number of provenance studies using seedlots from this collection have been established in different countries, and results reported—Toplu *et al.* (1987) in Turkey, Falkenhagen (1991) in South Africa, Jayawickrama & Balocchi (1993) in Chile, and Burdon *et al.* (1997) in New Zealand.

Of the three mainland populations, Monterey has often proved the best in trials. Shelbourne *et al.* (1979) concluded that it was the fastest growing native population over five sites in the New Zealand Genetic Survey at 6.5 to 7 years after planting, being at least as productive as the local land race on some lower-growth sites, although its relative superiority was smaller in two trials in Kaingaroa Forest at age 8 years (Burdon, Bannister & Low 1992). Burdon *et al.* (1997), over 22 sites in New Zealand, found Monterey to be best overall of the mainland populations for diameter at ages 6 to 11 years, particularly on some infertile sites. In height, it was also clearly superior on a few infertile sites but more often second to Año Nuevo. In five South African trials (Falkenhagen 1991), Monterey was overall the best of the three mainland populations at age 8 years, being significantly superior to Año Nuevo at three sites and Cambria at one site out of five. At age 6 years in three trials in Chile, Monterey was superior for volume, although not significantly different from the other mainland

populations (Jayawickrama & Balocchi 1993). It also ranked highest for growth traits in one trial in Turkey at age 6 years (Toplu *et al.* 1987).

Año Nuevo population material has often tended to be relatively poor for growth. This was so, especially for diameter and volume, across five sites in New Zealand (Shelbourne *et al.* 1979), but it was only slightly behind the other two mainland populations for mean diameter on two sites at age 8 years (Burdon, Bannister & Low 1992). It ranked best of the mainland populations for height over most of the New Zealand sites reported by Burdon *et al.* (1997), but was usually somewhat poorer than Monterey for diameter. In South Africa, Año Nuevo was inferior to Monterey and Cambria for growth traits at two of five sites (Falkenhagen 1991), especially those giving generally poor growth. In Turkey, this population was slightly inferior overall to Monterey in height, and inferior to Monterey and Cambria in mean diameter and stand volume (Toplu *et al.* 1987). It was also slightly poorer than the other mainland populations for mean tree volume in Chile (Jayawickrama & Balocchi 1993).

The growth of Cambria population material has proved variable in trials. In the New Zealand Genetic Survey and offshoot trials it was significantly inferior in growth at 7 years to Monterey at only one site and marginally better at two sites (Shelbourne *et al.* 1979). Burdon *et al.* (1997) found Cambria to be poorer than the other populations for height at all sites, appreciably so at about half of these. It was poorest at most sites for diameter, yet on infertile clay sites it was comparable in growth with Monterey and much better than Año Nuevo. Diameter growth at some sites was apparently depressed by past *Dothistroma* needle blight. In South Africa and Chile, Cambria was generally second to Monterey in growth and mostly superior to Año Nuevo (Falkenhagen 1991; Jayawickrama & Balocchi 1993). However, in California Guinon *et al.* (1982) found Cambria material inferior in growth to the other mainland populations, particularly Monterey, after eight growing seasons. In Turkey, it ranked lowest of the three for height but exceeded Año Nuevo considerably for diameter and stand volume (Toplu *et al.* 1987).

Shelbourne *et al.* (1979) noted a complex pattern of population  $\times$  site interaction evident from trials over five sites in New Zealand, although no formal analysis was given. Burdon, Bannister & Low (1992) found little population  $\times$  site interaction in trials including material from all five natural populations of *P. radiata*, over two contrasting sites on the New Zealand volcanic plateau. However, Burdon *et al.* (1997), in a study over a large number of sites in New Zealand, noted the poor performance of Año Nuevo on infertile clays in contrast to good performance on several other sites, as constituting a major interaction. Falkenhagen (1991) in South Africa, and Jayawickrama & Balocchi (1993) in Chile, concluded that provenance  $\times$  environment interaction was very minor for growth on the sites they sampled.

Most previous studies have found only weak evidence of subpopulation differentiation within populations in biochemical traits (Plessas & Strauss 1986; Moran *et al.* 1988; Burdon, Zabkiewicz & Andrew 1992), molecular traits (Strauss *et al.* 1993), or field growth traits (Hood & Libby 1980; Guinon *et al.* 1982; Falkenhagen 1991; Burdon, Bannister & Low 1992; Jayawickrama & Balocchi 1993; Burdon *et al.* 1997). Some subpopulation differences have been observed previously. Cromer *et al.* (1982) found differences in salinity tolerance among Monterey subpopulations. Toplu *et al.* (1987) noted some marked differences in 6-year volume among subpopulations within all three mainland populations, although the statistical significance was not given. Burdon, Bannister & Low (1992) found that a seedlot

from the Swanton locality (Año Nuevo) grew markedly more slowly than other natural seedlots from this population.

This paper reports the growth results from a series of eight trials of seedlots from the 1978 Eldridge-Firth collection, planted in 1979 in the State of New South Wales, Australia. Companion trials with similar natural population material were planted in other Australian States and New Zealand in 1980. The original aims of the experiment in New South Wales were to determine whether any of the natural populations were superior to the local land race or had characteristics that would make them immediately useful for inclusion in the local breeding programme, and to provide a resource of genetically diverse material for future selection in a long-term breeding programme. Because of the number and diversity of planting sites used, it also permitted a sensitive assessment of provenance  $\times$  environment interaction.

## MATERIALS AND METHODS

### Experimental Materials and Procedure

#### *Seedlots*

The seedlots used in these trials included 13 from the three natural populations in mainland California and one from a representative first-generation seed orchard (Table 1). There were four subpopulations from Año Nuevo population (designated 01-1 to 01-4), six from Monterey (02-1 to 02-6), and three from Cambria (03-1 to 03-3). The subpopulations were defined on geographical and ecological bases, but their boundaries were somewhat arbitrary. They have been described in detail by Eldridge (unpubl. data) and A. Firth (unpubl. data) and more briefly elsewhere (e.g., Cromer *et al.* 1982; Moran *et al.* 1988; Ades & Simpson 1991). Within each subpopulation, seed was collected from at least 22 trees. These trees were selected for having at least 40 collectable cones and being of large size and good form where possible. Trees sampled were separated by at least 100 m from one another. The reference seedlot (TSO) was collected in 1976 from the unculled first-generation Tallaganda Seed Orchard (Fielding 1964). The orchard was composed of 30 clones of first-generation select trees from plantations, 28 selected in the Australian Capital Territory, one in Victoria,

TABLE 1—Details of natural subpopulation seedlots included in this study

Population	Subpopulation No.	Collection location	Number of seed trees
Año Nuevo	01-1	Coastal strip	70
	01-2	Inland central	40
	01-3	Inland; south Swanton	40
	01-4	Inland northern	29
Monterey	02-1	Coastal, northern dunes	54
	02-2	Monterey Bay town	38
	02-3	Inland, Huckleberry Hill	36
	02-4	Inland, Jacks Peak	59
	02-5	Point Lobos-Yankee Point	22
	02-6	Carmel highlands	31
Cambria	03-1	Pico Creek	25
	03-2	Town area	50
	03-3	Scott Rock	25

and one in New Zealand. The orchard seedlot used in the present trials has been extensively used as a control in genetic tests in Australia.

### Nursery

Seedlings of all the seedlots were raised together at the CSIRO Division of Forestry nursery in Canberra, as first-year open-rooted stock in 14 unreplicated blocks.

### Trial design and sites

A series of eight trials was planted in New South Wales in winter 1979. At each site the trial was a randomised complete block design with 14 seedlots and 10 replicates of the 14 seedlots (13 subpopulations and control). Each plot was a row of five trees planted at a spacing of 2.5 m within rows and 3.0 m between rows.

Details of the eight planting sites are given in Table 2 and their locations are indicated in Fig. 1. The sites were not a random sample of those planted commercially. Rather, they were deliberately chosen to represent contrasting soil types or soil parent materials, and to span the range of sites and latitudes over which *P. radiata* was then planted in New South Wales. There is a general change in rainfall regime with latitude. In the north (Riamukka and Nundle sites) monthly averages tend to be high, with a slight summer maximum. Central tableland areas (Gurnang, Vulcan, and Hampton) have generally even but considerably lower monthly averages, with no marked seasonality. In the southern-most locations (Bondo, Green Hills, and Carabost) rainfall tends to be highest on average in winter to early spring, often with a summer-autumn drought (Table 2).

Data for soil or foliage nutrient levels have been collected from only one of the trial sites (Riamukka—foliage sampled at 3 years). Thus, detailed analysis of growth rate related to site nutrients in these trials was not possible. The Riamukka samples indicated high levels of nitrogen, phosphorus, potassium, and magnesium, consistent with the basalt geology of this site. Soil samples showing levels of phosphorus marginal for *P. radiata* growth have been incidentally collected fairly close to the Hampton trial (State Forests of NSW, unpubl. data). Retarded *P. radiata* growth has been found in lower-slope areas on acid volcanic (rhyolite) geology in Hampton State Forest (Ryan 1986).

TABLE 2—Provenance trial planting sites in New South Wales, listed in alphabetical order.

Site	Elevation (m)	Soil parent material	Soil texture*	Prior vegetation	Rainfall (mm)
Bondo (BON)	815	Gabbro	Clay loam	Improved pasture	1309†
Carabost (CBT)	605	Slates and siltstone	Light clay	First-rotation pine plantation	935†
Green Hills (GHL)	790	Granodiorite	Clay loam	Native forest	1306†
Gurnang (GUR)	1175	Siltstone	Light clay	Native forest	800‡
Hampton (HAM)	1100	Dacite	Clay loam	Native forest	850‡
Nundle (NUN)	1240	Greywacke	Loam	Native forest	1451†
Riamukka (RIA)	1250	Basalt	Clay loam	Native forest	1360†
Vulcan (VUL)	1010	Siltstone	Light clay	Native forest	750‡

\* Dominant texture of top 50 cm of soil profile, from analyses of samples within the regions of the trials

† Annual rainfall means from State Forests of NSW records, from sites in the same State Forests

‡ Annual rainfall means from rainfall isohyets, State Forests of NSW Bathurst Management Plan

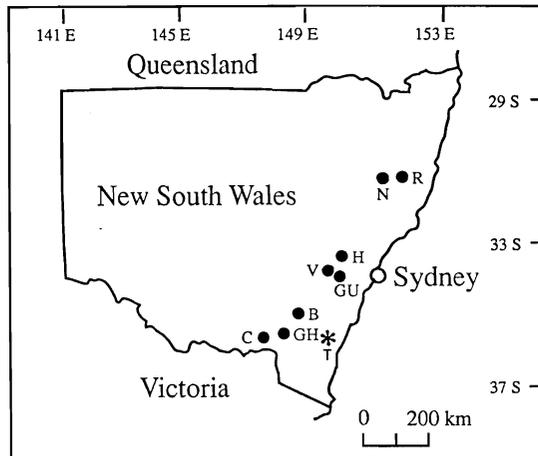


FIG. 1—Locations of provenance trial planting sites in New South Wales. From north to south: R = Riamukka; N = Nundle; H = Hampton; V = Vulcan; GU = Gurnang; B = Bondo; GH = Green Hills; C = Carabost. T = Tallaganda Seed Orchard, source of the control seedlot

Six of the trial sites were covered with native eucalypt forest before trial establishment. The forest at Green Hills, Nundle, and Riamukka was tall wet sclerophyll with a low shrub and grassy understorey; forest at Gurnang, Hampton, and Vulcan was a more stunted dry sclerophyll forest with a grassy understorey. This vegetation was cleared, windrowed, and burnt within the year prior to planting. The Bondo site carried highly improved pasture prior to trial establishment. The Carabost site had carried a first-rotation *P. radiata* plantation planted in the 1930s, the debris of which was broadcast-burnt after clearfelling a few months before trial establishment.

### Cultural treatments

Most of the trials received no fertiliser or herbicide treatments. Herbicide was applied only at Bondo, “Vorox” (amitrole) being sprayed in strips along the planting lines 2 months after planting, and “Gesaprim” applied 15 months after planting, to control pasture grasses. These treatments, similar to those applied to routine plantations nearby, were effective in allowing the pines to become successfully established. Fertiliser was applied at Bondo (boronated superphosphate at 100 kg/ha, 4 months after planting), at Carabost (100 g “Starter 15” (15:13:0:10 N:P:K:S) broadcast per tree, 4 months after planting), and at Vulcan (300 kg rock phosphate/ha applied from the air 18 months after planting). These were also routine treatments as applied to surrounding plantations.

### Assessments

The assessment reported was carried out between 8.0 and 8.3 years after planting at all sites except Nundle, where the trees were assessed at 8.8 years. Diameter over-bark at 1.3 m above ground-level (dbhob) and total height were measured on all trees, except those that were obvious runts or had been severely damaged by wind or snow. Survival ranged from 84% at Riamukka to 92% at Bondo and Nundle. The number of runts or severely damaged

trees was very low overall (1.2%), ranging from 0.3% at Nundle to 3.2% at Vulcan. The proportion of plots considered poorly stocked (three or fewer trees surviving of the five originally planted) varied from 6% at Bondo to 18% at Riamukka, with a mean of 12%. In two plots at Riamukka all trees had died, and data from another plot at Riamukka were omitted owing to an irretrievable recording error.

### Data Analysis

The arithmetic mean total height (HT) and equivalent basal area per hectare for each plot (BAHA), assuming a plot area of 37.5 m<sup>2</sup>/ha, were calculated. BAHA was based on the sum of the basal areas of the surviving trees in a plot. The square root of BAHA was used for subsequent analyses because this transformation stabilised residual variance across sites and resulted in the residuals being approximately normally distributed. HT was analysed without transformation. Analysis of variance for all seedlots, with the factors replicate, population, and subpopulation within population, was conducted within each individual site using the SAS GLM Procedure (SAS 1987). Population was considered to be a fixed effect, with replicates and subpopulations within populations random. An analysis across sites, using the SAS GLM Procedure (SAS 1987) with the native population data only, was conducted for each trait to test interactions of population × site, subpopulation × site, and replicate × population within site; a fully random model was used for this analysis, with the SAS Test option for estimation of the variance ratios. Expectations of mean squares (EMS) from the combined analysis are shown in Table 3.

## RESULTS

The results of the individual site analyses of variance for both HT and BAHA were very similar. Population differences were significant ( $\alpha=0.05$ ) for both traits at the same five sites.

TABLE 3—Expectations of Mean Squares (EMS) from the combined analyses of variance of height and square root basal area per hectare, assuming a fully random model.

Item	SAS GLM Type III EMS*
Site	$\text{Var}(\text{Error}) + 4.099 \text{ Var}(\text{REP} \times \text{POP}(\text{SITE})) + 9.966 \text{ Var}(\text{SITE} \times \text{PROV}(\text{POP})) + 40.987 \text{ Var}(\text{SITE} \times \text{POP}) + 12.265 \text{ var}(\text{REP}(\text{SITE})) + 122.65 \text{ Var}(\text{SITE})$
Replicate within site REP(SITE)	$\text{Var}(\text{Error}) + 3.988 \text{ var}(\text{REP} \times \text{POP}(\text{SITE})) + 11.963 \text{ Var}(\text{REP}(\text{SITE}))$
Population (POP)	$\text{Var}(\text{Error}) + 4.141 \text{ Var}(\text{REP} \times \text{POP}(\text{SITE})) + 9.966 \text{ Var}(\text{SITE} \times \text{PROV}(\text{POP})) + 41.409 \text{ Var}(\text{SITE} \times \text{POP}) + 79.728 \text{ Var}(\text{PROV}(\text{POP})) + 331.27 \text{ Var}(\text{POP})$
Subpopulation within population PROV(POP)	$\text{Var}(\text{Error}) + 9.973 \text{ Var}(\text{SITE} \times \text{PROV}(\text{POP})) + 79.781 \text{ Var}(\text{PROV}(\text{POP}))$
Site × Population SITE × POP	$\text{Var}(\text{Error}) + 4.141 \text{ Var}(\text{REP} \times \text{POP}(\text{SITE})) + 9.967 \text{ Var}(\text{SITE} \times \text{PROV}(\text{POP})) + 41.413 \text{ Var}(\text{SITE} \times \text{POP})$
Site × Subpopulation within population SITE × PROV(POP)	$\text{Var}(\text{Error}) + 9.975 \text{ Var}(\text{SITE} \times \text{PROV}(\text{POP}))$
Replicate × Population within site REP × POP(SITE)	$\text{Var}(\text{Error}) + 4.144 \text{ Var}(\text{REP} \times \text{POP}(\text{SITE}))$
Residual	$\text{Var}(\text{Error})$

\* From SAS GLM analysis, using TEST option for F-tests

Subpopulations within populations were significantly different at two sites—for HT at Nundle and Vulcan, and for BAHA at Green Hills and Hampton (Tables 4 and 5). Parallel analyses excluding the local Tallaganda seed orchard (TSO) control (data not presented) gave very similar results, except that subpopulation differences for HT were just non-significant at Vulcan ( $p=0.06$ ).

The across-site analyses revealed a highly significant population  $\times$  site interaction for both traits, but virtually no subpopulation  $\times$  site interaction (variance ratios were 1.09 and 1.05;  $p = 0.29$  and  $0.36$  respectively for the two traits—see Tables 6 and 7). Variance components for the subpopulation  $\times$  site interaction were correspondingly very small

TABLE 4—Analyses of variance for height (HT, in metres) of all seedlots (including TSO) at individual sites. The mean squares (MS) for each source of variation is followed by the variance ratio (F) and the probability (p) of a higher corresponding variance ratio. SAS Test option used to estimate variance ratios.

Source	df		Site							
			BON	CBT	GHL	GUR	HAM	NUN	RIA	VUL
Populations*	3	MS	18.53	2.51	2.12	2.05	5.10	15.95	16.19	7.58
		F	14.21	2.29	2.23	2.70	4.72	11.30	9.12	7.64
		p	0.00	0.14	0.15	0.11	0.03	0.00	0.00	0.01
Replicates	9	MS	1.91	1.18	1.12	3.67	6.62	0.78	3.72	9.56
		F	2.28	1.79	1.81	6.04	10.49	1.18	3.68	18.37
		p	0.02	0.08	0.07	0.00	0.00	0.31	0.00	0.00
Subpopulations within pop's	10	MS	1.30	1.09	0.95	0.76	1.08	1.41	1.77	0.99
		F	1.55	1.66	1.53	1.25	1.71	2.13	1.75	1.91
		p	0.13	0.10	0.14	0.27	0.09	0.03	0.08	0.05
Residual†	117	MS	0.84	0.66	0.62	0.61	0.52	0.63	0.66	1.01

\* Subpopulation mean square used as error for F-test.

† 114 residual degrees of freedom at Riamukka due to missing plots.

TABLE 5—Analyses of variance for square root of basal area (BAHA,  $m^2/ha$ ) of all seedlots (including TSO) at individual sites. The mean squares (MS) for each source of variation is followed by the variance ratio (F) and the probability (p) of a higher corresponding variance ratio. SAS Test option used for estimation of variance ratios.

Source	df		Site							
			BON	CBT	GHL	GUR	HAM	NUN	RIA	VUL
Populations*	3	MS	7.33	0.81	1.10	1.08	3.13	3.13	13.20	2.47
		F	9.80	2.27	1.34	2.57	4.82	62.78	24.05	10.03
		p	0.00	0.14	0.32	0.11	0.03	0.00	0.00	0.00
Replicates	9	MS	0.69	0.24	0.51	1.38	2.02	0.33	0.69	1.79
		F	1.29	0.76	1.30	5.11	8.66	0.87	1.31	8.00
		p	0.25	0.66	0.24	0.00	0.00	0.55	0.24	0.00
Subpopulations within pop's	10	MS	0.75	0.36	0.82	0.42	0.65	0.27	0.55	0.25
		F	1.40	1.14	2.10	1.56	2.79	0.71	1.04	1.10
		p	0.19	0.34	0.03	0.13	0.00	0.72	0.42	0.37
Residual†	117	MS	0.54	0.31	0.39	0.27	0.23	0.38	0.53	0.22

\* Subpopulation mean square used as error for F-test.

† 114 residual degrees of freedom at Riamukka due to missing plots.

TABLE 6—Analysis of variance for native population material across sites for height (HT, in metres)

Source	df	MS	Variance ratio	Probability	Variance component*
Site	7	764.83	84.07	0.00	6.160
Replicate within site	72	3.04	3.79	0.00	0.187
Population	2	22.20	2.18	0.14	0.036
Subpopulations within population	10	4.08	5.43	0.00	0.042
Population×Site	14	6.87	7.89	0.00	0.145
Subpopulations within population×Site	70	0.75	1.09	0.29	0.006
Replicate×Population within site	144	0.81	1.17	0.10	0.029
Residual	718	0.69			

\* From SAS GLM Type III EMS

TABLE 7—Analysis of variance for native population material across sites for square root of plot basal area (BAHA, m<sup>2</sup>/ha)

Source	df	MS	Variance ratio	Probability	Variance component*
Site	7	141.12	31.01	0.00	1.120
Replicate within site	72	0.80	2.16	0.00	0.035
Population	2	16.60	3.19	0.06	0.034
Subpopulations within population	10	1.42	3.81	0.00	0.013
Population×Site	14	4.15	10.69	0.00	0.091
Subpopulations within population×Site	70	0.37	1.05	0.36	0.002
Replicate×Population within site	144	0.37	1.04	0.36	0.004
Residual	718	0.35			

\* From SAS GLM Type III EMS

compared with those for population × site. Site differences were very major, with by far the largest variance components (Tables 6 and 7).

Means for populations, subpopulations, and the TSO control, as well as overall site means are shown in Tables 8 and 9. Site means varied greatly for both traits, the values for HT and BAHA at the lowest productivity site (Vulcan) being only 42% and 16%, respectively, of those at the most productive site. These highest productivity sites were Nundle and Bondo.

TSO had the largest population mean for both traits at all sites, although it was significantly better for HT than the next-best population only at Riamukka, and for BAHA at Nundle and Riamukka. Overall, Monterey was the best performer of the Californian populations, ranking second to TSO on five sites for HT and on six sites for BAHA. Año Nuevo tended to grow well on the more productive sites (Bondo and Nundle), but poorly on

TABLE 8—Population and subpopulation means for height (HT, metres) at each site.

Subpopulation	Site								Mean all sites
	BON	CBT	GHL	GUR	HAM	NUN	RIA	VUL	
<b>Año Nuevo</b>									
01-1	11.8	9.5	9.1	5.8	5.3	11.9	7.9	4.3	8.20
01-2	12.1	10.1	9.5	5.7	5.6	11.8	7.4	4.0	8.28
01-3	11.4	9.2	8.5	6.1	4.9	11.4	6.8	4.6	7.86
01-4	11.2	9.5	8.7	5.4	4.7	11.4	7.0	4.1	7.75
01 Mean*	11.6a	9.6b	9.0ab	5.8a	5.1b	11.6ab	7.3b	4.3b	
<b>Monterey</b>									
02-1	10.2	10.1	8.6	6.0	6.0	10.8	8.0	4.8	8.06
02-2	10.6	9.7	9.2	6.0	6.0	11.1	6.8	5.1	8.06
02-3	10.8	9.8	9.0	6.2	5.8	11.2	7.6	5.0	8.18
02-4	10.9	10.1	9.1	6.6	6.3	10.9	7.4	5.5	8.35
02-5	10.8	9.9	9.0	6.1	5.4	11.3	7.5	5.0	8.13
02-6	10.6	9.4	8.6	5.8	5.7	11.5	7.6	4.7	7.99
02 Mean	10.6b	9.8ab	8.9ab	6.1a	5.9a	11.1b	7.5b	5.0a	
<b>Cambria</b>									
03-1	9.6	9.2	8.3	5.4	5.5	9.5	6.2	4.1	7.23
03-2	10.6	10.1	8.8	6.0	6.0	10.4	6.5	4.9	7.91
03-3	10.1	9.8	8.6	5.9	5.7	10.8	6.0	4.3	7.65
03 Mean	10.1b	9.7ab	8.6b	5.8a	5.7a	10.3c	6.2c	4.4b	
p Subpop(pop)	0.13	0.10	0.14	0.27	0.09	0.03	0.10	0.05	
LSD ( $\alpha=0.05$ ) between subpop. means	0.8	0.7	0.7	0.7	0.7	0.7	0.9	0.6	0.17†
TSO	12.0a	10.5a	9.4a	6.4a	6.1a	12.4a	8.7a	5.6a	
Site mean	10.90	9.79	8.89	5.95	5.64	11.18	7.26	4.71	8.04

\* Population means followed by the same letter are not significantly different by t-test ( $\alpha=0.05$ ) using the corresponding subpopulation mean square from Table 4 as error.

† Appropriate for comparing subpopulations only within the same population.

some of the less productive sites (especially Hampton, where it was significantly poorer than Cambria, and Vulcan). Cambria, in general, performed poorly, with the lowest population rank for both traits at five sites; it grew worst, relative to the other populations, at the more productive sites but performed moderately well on some of the least productive sites (Carabost, Hampton, and Vulcan).

Individual subpopulations had means exceeding those of TSO at several sites, although never significantly so. Subpopulation 01-2 was taller than TSO at Bondo and Green Hills, and 02-4 had as large or larger BAHA at Carabost, Green Hills, Gurnang, Hampton, and Vulcan. It was also taller at Gurnang and Hampton.

The across-site analyses revealed highly significant differences for both traits between subpopulations within populations (Tables 6 and 7), although this was true for only a minority of individual trial sites (*see* Tables 4 and 5 and associated text). Subpopulations 01-1 and 01-2 from Año Nuevo were generally superior to 01-3 and 01-4. Among the Monterey subpopulations 02-4 was superior for growth, and overall averaged appreciably better than all the others (comparisonwise,  $\beta < 0.05$ ); its relative performance was best at sites

TABLE 9—Population and subpopulation means for square root of plot mean basal area (m<sup>2</sup>/ha) at each site.

Subpopulation	Site								Mean all sites
	BON	CBT	GHL	GUR	HAM	NUN	RIA	VUL	
<b>Año Nuevo</b>									
01-1	5.47	3.64	4.21	2.85	2.65	5.10	3.68	1.87	3.68
01-2	6.09	3.65	4.06	2.84	2.53	5.10	3.65	1.74	3.71
01-3	5.93	3.22	3.89	3.06	2.19	4.83	3.12	1.83	3.51
01-4	5.79	3.75	4.07	2.70	2.07	4.97	3.47	1.92	3.59
01 Mean*	5.82ab	3.57b	4.06a	2.86ab	2.36b	5.00b	3.48b	1.84b	
<b>Monterey</b>									
02-1	5.35	3.80	4.27	2.95	2.85	4.67	4.18	2.15	3.78
02-2	5.51	3.86	4.03	3.01	3.06	4.57	3.38	2.35	3.72
02-3	5.39	3.83	3.90	3.07	2.92	4.98	3.67	2.33	3.76
02-4	5.53	4.12	4.67	3.38	3.25	4.76	3.69	2.54	3.99
02-5	5.52	3.90	4.10	3.07	2.54	4.89	3.71	2.38	3.76
02-6	5.37	3.61	4.10	2.69	2.85	4.92	3.81	2.21	3.70
02 Mean	5.45b	3.85a	4.18a	3.03ab	2.91a	4.80b	3.74b	2.33a	
<b>Cambria</b>									
03-1	5.03	3.70	3.50	2.54	2.57	3.48	2.68	1.82	3.16
03-2	5.28	4.02	4.41	2.98	3.10	3.89	2.59	2.34	3.58
03-3	4.31	3.80	3.94	2.62	2.85	3.82	2.50	2.05	3.24
03 Mean	4.87c	3.84ab	3.95a	2.71b	2.84a	3.73c	2.59c	2.07b	
p Subpop(pop)	0.19	0.34	0.03	0.13	0.04	0.72	0.42	0.37	
LSD ( $\alpha=0.05$ ) between subpop. means	0.65	0.49	0.55	0.46	0.43	0.54	0.64	0.42	0.19†
TSO	6.27a	3.92a	4.57a	3.26a	3.14a	6.03a	4.65a	2.54a	4.29
Site mean	5.49	3.77	4.12	2.93	2.75	4.71	3.48	2.14	3.67
Actual basal area (m <sup>2</sup> /ha)	30.8	14.6	17.4	9.0	8.0	22.9	13.0	5.0	

\* Population means followed by the same letter are not significantly different by t-test ( $\alpha=0.05$ ) using the corresponding subpopulation mean square from Table 5 as error.

† Appropriate for comparing subpopulations only within the same population.

of lower productivity as measured by HT and BAHA, such as Vulcan and Gurnang (but also at Green Hills, for BAHA). The ranking of the Cambria subpopulations was identical for both traits at most sites, with 03-2 the best and 03-1 the worst.

## DISCUSSION

The highly variable growth rates (both in HT and BAHA) over the trial sites may be related partly to annual rainfall, although in the absence of rainfall figures for the actual sites a precise relationship cannot be established; certainly, the lower rainfall sites generally displayed the poorer growth. Site factors related to geology probably had an influence. *Pinus radiata* plantations in lower slope areas on Silurian-Devonian rhyolite geology in Hampton State Forest have been found to exhibit depressed BAHA growth (Ryan 1986). It is reasonable to consider the nearby Hampton provenance trial site, on similar acid volcanic parent material and slope position, to be intrinsically poor for pine growth. Ridge sites on

siltstone geology in the Bathurst area, with shallow, gravelly soils (generally similar to the Gurnang and Vulcan sites in this study) have also been associated with poor growth of *P. radiata* (Ryan 1986).

The TSO seedlot showed considerable stability in growth across the range of trial sites, outperforming nearly all of the subpopulations at each site. Although the seed orchard was composed mostly of selections from a limited geographical area near Canberra, its seedling stock appeared well adapted for growth across sites with quite widely varying climatic and soil conditions. The TSO population originated from Monterey or Año Nuevo, or as a mixture of both (Moran & Bell 1987). Plantations in southern Australia in which the orchard clones were selected underwent two or three generations of natural and silvicultural selection and one generation of intense artificial selection for growth rate, improved stem form, and small-diameter branching. In several other field trials in south-eastern Australia (e.g., Matheson *et al.* 1986; Johnson 1991), bulk TSO stock has proved superior in growth to most unimproved seedlots and to most other Australian first-generation seed orchard lots.

The overall superiority of Monterey population material, compared with the other natural populations in these trials, accords with results from most previous studies (Shelbourne *et al.* 1979; Toplu *et al.* 1987; Falkenhagen 1991; Burdon, Bannister & Low 1992; Jayawickrama & Balocchi 1993; Burdon *et al.* 1997, for diameter). Its good adaptability to lower-productivity sites, apparent in this study, was noted also by Shelbourne *et al.* (1979) and Burdon *et al.* (1997) in New Zealand. The latter authors noted a “very marked” superiority of Monterey over Año Nuevo and even New Zealand land race material on infertile clay soils.

Año Nuevo grew best of the native populations on the sites of highest productivity (Bondo and Nundle), and may be best adapted to more fertile sites. Burdon *et al.* (1997) considered this to be so in New Zealand, where the population performed poorly on infertile clays. It showed adaptive advantages in the South Island, including areas of snow hazard. In the study of Falkenhagen (1991), Año Nuevo grew most poorly on two badly-drained sites with low rooting depth, which reduced the growth of all populations. It was inferior to both Monterey and Cambria in Chile (Jayawickrama & Balocchi 1993) and Turkey (Toplu *et al.* 1987). The Turkish site was fairly dry with clay soil and low growth rates similar to the least productive New South Wales sites such as Vulcan.

The considerable inferiority of the Cambria population material on the more productive and/or fertile sites in the present study (Bondo, Nundle, Riamukka) was more marked than in some overseas trials of a similar or slightly younger age (Shelbourne *et al.* 1979; Burdon, Bannister & Low 1992; Falkenhagen 1991). Burdon *et al.* (1997) noted that Cambria was the poorest population for diameter at about half of 19 sites in New Zealand, but grew as well as Monterey on infertile clay soil sites. The poor performance of the Cambria trees on certain sites in the present trials, and the highly significant population  $\times$  site interaction observed, may be due partly to *Dothistroma* needle blight. Severe recurrent epidemics of *Dothistroma* occurred at Nundle and Riamukka from 3 years after planting. *Dothistroma* was also present at Bondo, Green Hills, and Carabost, but severe epidemics did not occur until the trials there were older than 8 years, and so would not have materially affected growth results at these sites. Cambria is the most susceptible population of those tested, and TSO the least susceptible (Ades & Simpson 1991). Cambria grew very poorly and TSO well at both Nundle and Riamukka, consistent with their relative susceptibilities. However, the disease could not explain the similarly poor performance of Cambria at Bondo.

The results for genotype  $\times$  environment interaction in the present experiment differ in several ways from most previously published studies of natural *P. radiata* provenances. The first difference is that there was a large and statistically significant population  $\times$  site interaction for both height and basal area. Falkenhagen (1991) in South Africa, Burdon, Bannister & Low (1992), and Jayawickrama & Balocchi (1993) in Chile, concluded that provenance  $\times$  environment interaction was minor for growth on the sites they sampled. Burdon *et al.* (1997) considered that the variable performance of Año Nuevo over different site types represented a major interaction. The difference between this study and several previous ones may be largely related to the very wide range of productivity among the planting sites represented in this study. Between the most productive and least productive sites, HT at 8 years varied by a factor of 2.3, and untransformed BAHA by a factor of 6.2 (Tables 8 and 9). Sites giving growth rates as poor as Gurnang, Hampton, and Vulcan probably would not be considered for planting in most commercial programmes, and so would usually not be sampled in experiments. Cambria tended to perform relatively well, and Año Nuevo poorly, on these sites of very low productivity.

The second way in which these results differ from many previous results is that there appeared to be some marked differences between subpopulations within populations. Most previous studies have found only weak evidence of subpopulation differentiation in field growth traits (Hood & Libby 1980; Guinon *et al.* 1982; Falkenhagen 1991; Burdon, Bannister & Low 1992; Jayawickrama & Balocchi 1993; Burdon *et al.* 1997). Toplu *et al.* (1987) noted some marked differences in 6-year volume among subpopulations within all three mainland populations, although the statistical significance was not given. Burdon, Bannister & Low (1992) found that a seedlot from the Swanton locality (Año Nuevo) grew markedly more slowly than other natural seedlots, and Burdon *et al.* (1997) noted subpopulation 01-3 (from Swanton) as showing slower height growth than subpopulations 01-1 and 01-2 on most sites. This trend was also evident in most of the present trials. If the differences in the performance of Año Nuevo subpopulations in New South Wales are due to adaptation and not to variation in average inbreeding, then selection may have been very strong to overcome gene flow and cause differentiation over small distances in this natural population of a wind-pollinated, predominantly outcrossing species.

The obvious superiority of subpopulation 02-4 (Monterey) in five of the present trials was reflected in Turkey (Toplu *et al.* 1987), but not in the South African study (Falkenhagen 1991) nor in Chile, where subpopulation 02-1 was superior (Jayawickrama & Balocchi 1993). Subpopulation 03-2 was superior among the Cambria seedlots in South Africa and in Chile, though less strongly than in these trials.

Monterey subpopulation 02-4 in particular appears to have scope for use in *P. radiata* breeding in New South Wales. It outgrew the local improved TSO stock on several of the less productive trial sites. Burdon (1992) and Burdon *et al.* (1997) considered that increased representation of Monterey population material in the New Zealand breeding programme was desirable, mainly because of its relatively good growth on phosphorus-deficient clay soils and its resistance to needle-cast fungi, and recommended further testing of this population on northern New Zealand sites. Four of the five New South Wales sites where 02-4 grew well (Carabost, Gurnang, Hampton, and Vulcan) had low productivity, possibly due to relatively low rainfall and fertility. Thus there is a possibility that using intensively selected and fully outbred material of natural Monterey origin (and possibly also Cambria

origin—see later discussion) could improve the productivity of *P. radiata* plantations on drier sites with nutrient levels limiting to tree growth.

It is very unlikely that there was any Cambria material in the original introductions from which Australian plantations and breeding populations were derived (Moran & Bell 1987; J.M. Fielding pers. comm.). Cambria as a pure population of *P. radiata* has generally been regarded as not commercially useful. This perception was probably engendered in part by the poorer health and growth rate of Cambria trees, relative to those from the other mainland populations and local stock, in early plantings over a number of sites in the Australian Capital Territory (Fielding 1961; Doran 1974). More recently, Cambria population material has been regarded as possibly useful as a source of genes for tolerance to Phytophthora root rot (Butcher & Stukely 1986), improved stem form and tolerance to phosphorus-deficient soils, (Burdon *et al.* 1997), and tolerance to soil salinity (Cromer *et al.* 1982).

The growth results for Cambria material in these trials, and the implication of severe Dothistroma epidemics in its poor performance at Nundle and Riamukka, indicate that this population (particularly selections from subpopulation 03-2) may be useful on some sites where Dothistroma is not a problem. The sites where Cambria performed relatively well (Carabost, Hampton, and Vulcan) have low annual rainfalls relative to the other sites (except Gurnang) and possibly sub-optimal fertility for *P. radiata*. The result is consistent with the observation that Cambria material is capable of growing well on phosphorus-deficient clays in New Zealand (Burdon 1992), and with its superior performance over Año Nuevo on a clay soil with low productivity in Turkey (Toplu *et al.* 1987). Interpopulation hybrids including Cambria have grown well in comparison with pure Monterey population trees in a trial planted in 1973 on a fertile site in New South Wales (K.G. Eldridge unpubl. data). Such hybrids may combine better adaptation to certain environments with higher general growth rates, and could prove very useful in a generally adapted breed of *P. radiata*.

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