

PROVENANCE VARIATION IN NEW ZEALAND-GROWN *EUCALYPTUS DELEGATENSIS*. 1: GROWTH RATES AND FORM

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ABSTRACT

Eucalyptus delegatensis R.T.Baker provenance trials, at two sites in New Zealand, were assessed at age 8 years for growth (diameter) and form (primarily stem straightness). Tasmanian provenances overall had slightly larger ($p < 0.1$) diameters than Australian mainland provenances, but were significantly ($p < 0.0001$) poorer in form than mainland ones. The results for diameter growth at age 8 were in contrast to those for earlier (age-3) height. In both results at age 3 on the two New Zealand sites and the published results of the same material on four trial sites in south-eastern Australia, Victorian provenances had clearly excelled Tasmanian provenances. Hence, Victorian provenances that show rapid early growth may later be overtaken by Tasmanian provenances.

New Zealand seedlots (commercial lots and open-pollinated families) showed, on average, modest diameter but good form, in line with their predominantly New South Wales origins. The families varied strongly in both diameter and form.

Keywords: provenance; variation; growth rate; tree form; *Eucalyptus delegatensis*.

INTRODUCTION

Eucalyptus delegatensis occurs naturally in moderate- to high-altitude regions of south-eastern Australia (Fig. 1) in New South Wales (including Australian Capital Territory), Victoria, and Tasmania (Moran *et al.* 1990). It is found between latitudes approximately 35° and 43°S with an overall altitudinal range of 160–1500 m. The optimal altitudinal range, however, is 900–1400 m on the mainland and 300–900 m in Tasmania. The species occurs in tall, somewhat open forests, and is commercially important for both sawn timber and pulp, especially in Tasmania.

Australian mainland and Tasmanian populations of *E. delegatensis* show various important and consistent differences. Boland & Dunn (1985) showed, using cluster analysis, that mainland and Tasmanian populations had distinctive floral, vegetative, and physiological

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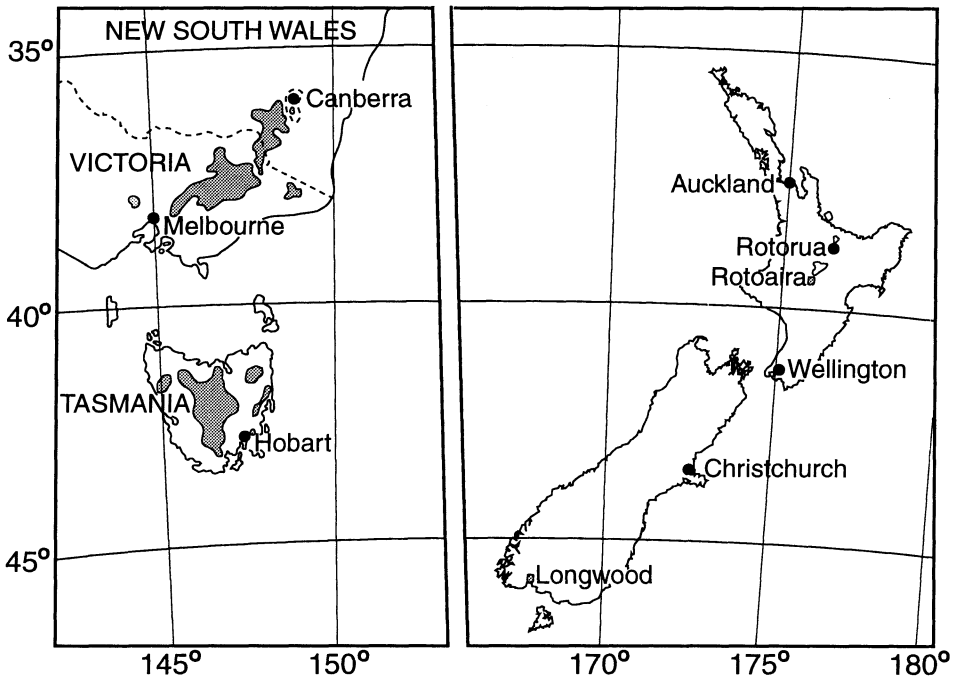


FIG. 1—Natural distribution of *E. delegatensis* and location of trial sites.

features. Boland (1985) also demonstrated differences in seedling characteristics between mainland and Tasmanian sources and, on all this evidence, formally segregated the Tasmanian material populations as a separate sub-species, *E. delegatensis* subsp. *tasmaniensis*. Genetic differentiation between Tasmanian and mainland material has also been confirmed by an allozyme study (Moran 1992).

Exotic plantations of *E. delegatensis* have been established in Chile, New Zealand, South Africa, and Spain. The species appears well suited to parts of New Zealand (especially in southern latitudes) and is popular because of its fast growth, easy establishment, good frost tolerance, and form characteristics (relatively good for one of the ash-group eucalypts). *Eucalyptus delegatensis* was for a while the most commonly planted eucalypt in New Zealand State forests (Wilcox 1980). Recently, *E. nitens* (Deane et Maiden) Maiden has become the preferred eucalypt for the cooler New Zealand sites because of its dependably rapid growth and the successful biological control of the insect pest *Paropsis charybdis* Stål, but *E. delegatensis* remains of interest in case new problems arise with *E. nitens*.

Provenance trials for *E. delegatensis* were established in New Zealand in 1978 from a large and comprehensive collection made available by CSIRO Division of Forest Research (D.J.Boland pers. comm.). Early (age-3) assessments of these trials showed provenances from Southern Victoria to be superior overall and Victorian provenances in general to be superior to those from Tasmania and New South Wales (Forest Research Institute 1983). Moran *et al.* (1990) reported age-3 results from Australian trials (Tasmania and New South Wales) of this collection. Their results also showed an overall superiority of Victorian

sources, with particular sources such as Royston River (near Taggerty, Vic.) and Ada River (near Powelltown, Vic.) ranking top as they also did on the North Island site of the New Zealand trials. Moran *et al.* (1990) concluded that for growth performance there appeared to be clear groupings of provenances of *E. delegatensis* from defined geographic regions. Such groupings have not been commonly reported with other species, especially low-altitude species (Moran *et al.* 1990; Burgess 1988; Griffin *et al.* 1982).

In this paper we report results from an assessment of diameter and form of this provenance material made at age 8 on two sites, and compare these results with the earlier assessments both on the New Zealand sites and on Australian sites.

MATERIALS AND METHODS

Trials and Assessments

The material for this study has been described by Boland *et al.* (1980) and was from a detailed range-wide collection from throughout Tasmania, Victoria, New South Wales (NSW), and the Australian Capital Territory (ACT). Each native provenance origin was represented as a bulked seed collection of naturally pollinated seed from 5–10 trees (Boland *et al.* 1980). In addition, seed from seven New Zealand sources and 46 plus-tree families was included (Appendix 1).

These seedlots were divided into four sets of 36 seedlots each (Appendix 1). Sets 1 and 2 were from the Australian provenance collection except for seven New Zealand seedlots (mainly commercial collections). Set 3 was a mixture of Australian provenance material and 10 New Zealand plus-tree selections. Set 4 was entirely of New Zealand origin. Planting was done in November 1978, with stock grown in jiffy pots at separate nurseries for the respective planting sites. Randomisation was not attempted in the nurseries, but boxes of the provenance lots were periodically moved in order to even out environmental effects.

The two sites reported here (Fig. 1) were at Rotoaira in the central North Island (lat. 39°00'S; alt. 700 m; precipitation c. 2000 mm; soil derived from fairly coarse rhyolitic pumice) and Longwood Forest in Southland (lat. 46°30'S; alt. 230 m; precipitation c. 1200 mm; soil derived mainly from schist loess) (Wilcox *et al.* 1985).

At Rotoaira all four sets were established. The trial layout was a randomised complete block design with 36 replicates (reps) of single-tree plots; the sets were grouped into separate rep/set blocks, with a split-plot feature that could, for our purposes, be disregarded. For the Longwood trial only set 1 was available; a randomised complete block design was used, with 27 reps and one tree per seedlot per rep.

An age-3 assessment for height growth had been made at both sites (Forest Research Institute 1983, Wilcox *et al.* 1985), soon after the Rotoaira trial had suffered about 12% losses through wind damage.

The age-8 assessment included recording:

- diameter (cm) outside bark at breast height (1.4 m)
- stem straightness (visual scores 1–9, 9 being best).

Also scored visually at Rotoaira, but not reported in detail, were incidence of flowering and branch habit quality. All living trees were assessed except those that were suppressed or significantly damaged.

At Longwood the trees were about 14 m tall and uniformly vigorous; at Rotoaira they were smaller, and appreciably nitrogen-deficient in much of the trial. Effective net survivals (percentage of trees planted deemed assessable) were 75% at Rotoaira and 80% at Longwood.

Statistical Analysis

For each site the data were subjected to analysis of variance (ANOVA) using PROC GLM of the SAS statistical system (SAS Institute 1989). For Rotoaira, separate ANOVAs were carried out for:

- (1) Provenances only, with the following effects: reps, sets, reps \times sets, provenances.
- (2) Open-pollinated (OP) families (from New Zealand sources only, Sets 3 and 4) with the following effects: reps, sets, reps \times sets, families.

Reps and regions were effectively fixed effects. Reps \times sets, while effectively random, reflected block environmental effects along with reps, which could be partitioned off. In the event, set effects proved negligible.

For Longwood the basic ANOVA model was straightforward, containing only effects of reps and provenances.

For the native provenances, the provenances effect could be partitioned into regional groups (i.e., regions) and provenances(regions) effects, regions being clearly a fixed effect and provenances(regions) conservatively treated as a random effect. Alternative regional groupings for the native provenances were:

- (i) Regions (Fig. 1), namely, New South Wales including Australian Capital Territory (NSW), Victoria (VIC), and Tasmania (TAS)—2 degrees of freedom (df).
- (ii) Combined regions, namely, MAINLAND and TASMANIA—1 df.

An additional group comprised the seven New Zealand composite seedlots. For regional groups, standard errors, based on provenance-mean variation, could be calculated and used for t-tests in pairwise comparisons of group means.

Cross-reference of performance, for a trait, between the two sites, was addressed by calculating Type B genetic correlation estimates (Burdon 1977), dividing correlations of seedlot means between the sites by the square root of the product of repeatabilities of means at the respective sites. (Repeatability of means was given by $(F - 1)/F$, F being the variance ratio in the test for seedlot differences.) Departures of such genetic correlations below +1 reflect genotype-site interactions that can change seedlot rankings according to site. This analysis was extended to age-3 data, which also included results for 64 provenances on Australian sites (Moran *et al.* 1990; G.F.Moran pers. comm.), and separate correlation estimates were also made within the main provenance groups.

Cross-reference of age-8 diameter with age-3 height records (Forest Research Institute 1983; Wilcox *et al.* 1985) was made in two ways. One way was to estimate genetic (i.e., provenance) correlations between the two variables. Within-site estimates (Type A, Burdon 1977) were based on data from the same individuals and were obtained from analyses of variance for the respective variables and of cross-products of the two variables (*after* Falconer 1981; Becker 1984). Across-site estimates (Type B, Burdon 1977) were estimated as described earlier; departures of correlations below +1 reflect some combination of imperfect within-site correlation and genotype-site interaction. The second approach was to

repeat the ANOVAs of age-8 diameter, as analysis of covariance (ANCOVA), adding age-3 height to the model as a covariate; this helped to define any patterns of change in comparative performance.

RESULTS

Provenance Variation in Age-8 Diameter and Bole Straightness

Differences among native provenances for age-8 diameter were pronounced ($p < 0.001$) at Rotoaira but only weakly expressed and not statistically significant ($p > 0.05$) at Longwood (Table 1). Differences among regions, however, were not statistically significant (although the deliberate geographic spread of provenances within each region will presumably have made this test over-stringent). Provenances within regions showed extremely significant differences at Rotoaira ($p < 0.0001$) but not at Longwood ($p > 0.05$).

Comparing combined regional group means (Table 2), TASMANIA material showed marginally greater mean diameters than MAINLAND. Within MAINLAND, VIC showed a marginally higher mean than NSW. The NZ origin group was marginally lowest at Longwood, and lowest equal at Rotoaira.

Straightness scores showed marked provenance differences, mainly among regions (Table 1). The main differentiation was between MAINLAND and TASMANIA, MAINLAND being markedly superior (Table 3). In other group comparisons (Table 3), VIC averaged slightly better than NSW, and the NZ origin lots were slightly inferior on average to both these MAINLAND groups.

TABLE 1—Analyses of variance for age-8 diameter (cm) and straightness score (1–9) at Rotoaira and Longwood for native provenance seedlots.

Item	Degrees of freedom	Diameter			Straightness		
		Mean square	F	P	Mean square	F	P
Rotoaira							
Reps	35	18.29	2.31	****	16.18	5.48	****
Sets	2	61.83	0.92†	NS	7.20	1.02†	NS
Reps × sets	69	47.39	5.98	****	7.95	2.70	****
Provenances(sets)	88	28.05	3.54	***	14.25	4.83	***
Regions	2	30.99	1.11	NS	539.63	89.6	****
Provenances(regions)	86	27.98	3.52	****	2.03	2.03	****
Error	2200	7.93			2.95		
Longwood							
Reps	26	24.72	2.20	***	14.03	3.60	****
Provenances	31	15.05	1.34	NS	15.20	3.91	****
Regions	2	35.38	2.59	NS	140.39	21.0	****
Provenances (regions)	29	13.65	1.21	NS	6.57	1.69	*
Error	629	11.26			3.90		

NS p (probability > F under null hypotheses) > 0.05

* $p < 0.05$

*** $p < 0.001$

**** $p < 0.0001$

† Satterthwaite-type approximate test: (SAS (SAS Institute 1989) PROC GLM, RANDOM statement, TEST option)

TABLE 2—Regional provenance group means \pm standard errors for stem diameter (cm), and results of *t*-tests [error = provenances (groups)] for group differences.

Group	Site	
	Longwood	Rotoaira
MAINLAND	16.7 \pm (0.17)	14.2 \pm (0.13)
TASMANIA	17.4 \pm (0.26)	14.6 \pm (0.19)
p (difference = 0)	0.02	0.08
VIC	16.9 \pm (0.22)	14.4 \pm (0.17)
NSW	16.4 \pm (0.25)	13.9 \pm (0.21)
p (difference = 0)	0.15	0.1
NZ sources	16.2 \pm (0.40)	13.9 \pm (0.38)

TABLE 3—Regional provenance group means \pm standard errors for stem straightness score, and results of *t*-tests [error = provenances (groups)] for group differences.

Group	Site	
	Longwood	Rotoaira
MAINLAND	6.35 \pm 0.115	6.48 \pm 0.061
TASMANIA	4.93 \pm 0.184	5.04 \pm 0.088
p (difference = 0)	<0.0001	<0.0001
VIC	6.39 \pm 0.153	6.51 \pm 0.078
NSW	6.30 \pm 0.175	6.43 \pm 0.096
p (difference = 0)	>0.5	>0.5
NZ sources	6.30 \pm 0.276	6.30 \pm 0.178

Branch habit quality scores (details not shown) showed less-pronounced seedlot differences than stem straightness scores, but otherwise showed closely parallel variation. In particular, the scores were better for MAINLAND than for TASMANIA material.

Between the two sites, age-8 diameters appeared to be closely correlated; while the correlation of provenance/seedlot means was only 0.30 ($p=0.07$) the estimated genetic (i.e., seedlot) correlation was 0.73. This is consistent with generally high genetic correlations that were observed for age-3 height among both New Zealand and Australian sites (Table 4).

Age-8 Diameters in Relation to Age-3 Heights

Provenance-mean correlations between age-3 heights and age-8 diameters were mostly weak (Table 5). Even the estimated genetic correlations, which were imprecise, tended to be low, and two were negative (Table 5).

Table 6 shows the results of ANCOVA, adjusting age-8 diameter for individual covariance on age-3 height. This revealed much stronger region effects in the covariance-adjusted model, spotlighting a change in relative performance of the regions. Also noticeable, although less marked, was the sharper resolution after the covariance adjustment of provenance differences within regions.

TABLE 4—Between-site correlations for age-3 height (bold type): seedlot-mean correlations above diagonal, Type B genetic (i.e., seedlot) correlation estimates below diagonal. Numbers of pairs of observations in ordinary type.

	ROTO	LONGW	PILOT	MYRTL	TARRA	PARRA
ROTO	1	0.59*** 30	0.72**** 58	0.74**** 54	0.81**** 56	0.51**** 56
LONGW	0.76	1	0.30NS 29	0.65*** 27	0.59** 26	0.52** 26
PILOT	0.90	0.44	1	0.42** 51	0.47** 52	0.36** 52
MYRTL	0.97	0.99	0.61	1	0.74**** 52	0.60**** 51
TARRA	1.05	0.89	0.68	1.10	1	0.46*** 55
PARRA	(genetic correlation estimates not available)					

Sites: LONGW = Longwood Forest, Southland NZ; ROTO = Rotoaira, central North Island, NZ; PILOT = Pilot Hill, NSW (Moran *et al.* 1990); MYRTL = Myrtlebank, Tasmania (Moran *et al.* 1990); TARRA = Tarraleah, Tasmania (Moran *et al.* 1990); PARRA = Parrawe, Tasmania (Moran *et al.* 1990).

NS p ($p = \text{probability } \rho = 0$) > 0.05

** $p < 0.01$

*** $p < 0.001$

**** $p < 0.0001$

NOTE: Estimates of genetic correlations are approximate and alternative solutions may exist (Burdon 1991)

The changes in growth performance over time are also shown quite dramatically in the rankings of provenance lots for age-8 diameter (Table 7) and in the actual means (Appendix 1). In the 62 provenance seedlots that were represented on at least two of six sites (the two New Zealand and four Australian sites) for the age-3 rankings (Table 7) Victorian provenances provided 13 of 15 seedlots in the top quartile of rankings, while Tasmanian provenances provided 10 of 15 seedlots in the bottom quartile, the other five being NSW seedlots. This stratification was no longer apparent in the age-8 rankings. Only one Tasmanian seedlot was in the bottom quartile at age-8 and seedlots 127 (Royston River) and 130 (Ada River), which had been ranked either 1 or 2 on all six sites based on age-3 heights (Table 7), were in the bottom quartile of rankings based on age-8 diameter (Appendix 1). Meanwhile, provenance seedlots from Tasmania such as Bendover Hill (seedlot 157, Appendix 1) and Ben Nevis (seedlot 38, Appendix 1) were top-ranked based on age-8 diameters. Ben Lomond, Tasmania which was bottom-ranked at age-3 (Table 7) was in the second quartile overall and in the top quartile at Rotoaira at age 8 (Appendix 1).

Performance of New Zealand Seedlots

In the New Zealand material both the composite seed lots (Tables 2 and 3) and the OP family lots were very similar in average diameter and stem straightness score to the NSW seedlots, which ranked relatively low for diameter but well for straightness. Among the composite seedlots only that from Karioi Forest (No.95, Appendix 1) ranked highly for stem diameter.

TABLE 5—Sample correlations (bold type) of seedlot means for age-3 height with age-8 diameter between and within sites. Genetic correlation estimates (Type B) in parentheses. Numbers of pairs of observations and probability levels (p) indicated in ordinary type.

Age-3 height	Age-8 diameter					
	All seedlots		Tasmanian		Mainland	
	ROTO†	LONGW	ROTO	LONGW	ROTO	LONGW
ROTO	0.16 (0.14)‡ 62 NS	-0.15(-0.28) 30 NS	0.19 22 NS	0.09 9 NS	0.32 40 *	0.05 21 NS
LONGW	0.23 (0.27) 30 NS	0.50 (0.71)‡ 30 **	-0.34 9 NS	0.02 9 NS	0.45 21 *	0.68 21 ***
PILOT	-0.22 (-0.40) 58 NS	-0.19 (-0.32) 29 NS	0.09 22 NS	0.45 9 NS	-0.22 36 NS	0.13 20 NS
MYRTL	0.21 (0.33) 54 NS	0.01 (-0.01) 27 NS	0.19 21 NS	0.38 9 NS	0.27 33 NS	0.07 18 NS
TARRA	0.30 (0.47) 56 *	0.20 (0.43) 26 NS	0.01 21 NS	0.57 9 NS	0.50 35 **	0.33 17 NS
PARRA	-0.013 56 NS	0.10 26 NS	0.18 21 NS	0.14 9 NS	-0.05 35 NS	0.14 17 NS

NS p (p = probability $\rho = 0$) >0.05

* p < 0.05

** p < 0.01

*** p < 0.001

† See Table 4 for key to sites

‡ Type A (within-site) genetic correlation estimates (Burdon 1977), for which no good test of significance exists.

Note: Estimates of between-site genetic correlations are approximate and alternative solutions exist (Burdon 1991).

TABLE 6—Results of analyses of covariance (ANCOVA) of age-8 diameter adjusting for individual covariance on age-3 height, compared with results of ANOVAs (Table 3) on unadjusted diameter.

Item	ANOVA				ANCOVA			
	Degrees of freedom	Mean square	F	P	Degrees of freedom	Mean square	F	P
Rotoaira								
Regions	2	30.99	1.11	NS	2	346.27	130.0	****
Provenances(regions)	86	27.98	3.52	****	86	29.67	4.63	****
Error	2200	7.93			2199	6.42		
Longwood								
Regions	2	35.38	2.59	NS	2	97.04	8.16	***
Provenances(regions)	29	13.65	1.21	NS	29	11.89	1.92	***
Error	629	11.26			628	6.20		

NS p (probability > F under null hypotheses) >0.05

*** p < 0.001

**** p < 0.0001

TABLE 7—Rankings of seedlots for age-3 heights from the two New Zealand, and four Australian trials (Moran *et al.* 1990). The 62 seedlots listed here are those which are represented in both New Zealand and Australian sites. Ranks were re-scaled to 62 (SAS [SAS Institute 1989] PROC RANK, TIES = HIGH) and are ranked overall on the average re-scaled ranking across sites.

Provenance		Region	Average	Seedlot rankings on sites*					
No.	Origin			ROTO	LONGW	PILOT	MYRTL	TARRA	PARRA
130	Ada River	VIC	7	1	4	27	1	1	8
127	Royston River	VIC	7	2	32	1	2	5	2
133	Mt Ewen	VIC	8	10	8	3	13	2	11
129	Mt Macedon	VIC	9	8	2	20	9	13	1
134	Mt Baldhead	VIC	10	13	-	13	10	4	8
162	Mt Ellery	VIC	10	9	12	16	11	3	-
164	Cromwell Knob	VIC	10	5	-	-	20	8	8
121	Beecher Hill	VIC	12	11	-	13	-	-	-
123	Big Hill	VIC	13	3	-	8	12	9	32
111	Geehi	NSW	13	6	-	2	14	32	13
120	Mt Wills	VIC	14	7	-	6	25	16	15
131	Mt Useful	VIC	15	17	38	23	3	6	4
132	Mt Skene	VIC	16	15	10	5	20	13	33
142	Surrey Hills	TAS	17	26	22	37	4	11	3
124	Big Ben	VIC	20	22	24	9	24	34	5
128	Lake Mountain	VIC	20	4	-	26	48	7	16
144	Luina	TAS	21	20	-	37	5	19	22
110	Youngal	NSW	22	23	14	21	24	26	24
158	Mt Gibbo	VIC	24	12	-	-	32	22	29
159	Forlorn Hope Tk	VIC	25	33	-	-	29	29	9
113	Dargals Range	NSW	26	19	-	4	35	55	15
157	Bendover Hill	TAS	26	21	-	44	8	33	26
126	Upper Howqua	VIC	27	14	48	10	28	46	13
105	Clear Ck.	NSW	28	24	-	14	52	24	25
116	Yarrangobilly	NSW	28	25	40	19	-	-	-
125	Razorback Spur	VIC	30	47	26	18	34	38	18
139	Dazzler Range	TAS	30	35	-	43	18	19	37
141	Maggs Mt	TAS	31	32	28	41	51	15	17
122	Mt Buffalo	VIC	32	41	46	7	17	32	46
109	Cascade	NSW	32	16	-	35	41	25	43
143	Yellow March Rd	TAS	32	37	-	51	6	47	19
151	Russell River	TAS	32	55	8	49	24	28	28
153	Middle Peak	TAS	32	31	-	54	16	14	47
117	Gungarlin River	NSW	33	18	-	32	40	36	38
149	Mt Dromedary	TAS	33	36	-	45	32	17	36
107	Mt Nurenmerenmang	NSW	34	42	-	11	36	58	23
161	Mt Delegate	NSW	35	27	52	22	27	23	56
135	Hartz Mts	TAS	35	34	18	48	37	27	44
102	Leura Gap	ACT	37	39	-	30	-	21	57
148	Tunbridge Tier	TAS	39	51	-	46	34	35	27
106	The Granites	NSW	39	43	-	17	-	37	58
112	The Pinnacle	NSW	39	38	58	29	42	45	22
119	Pilot Hill	NSW	40	50	30	24	48	50	35
160	Bulls Head	ACT	41	46	34	26	58	-	-
163	Nunniong Plateau	VIC	42	29	36	-	-	40	61
140	Cluan Tie	TAS	42	60	-	43	27	39	40
104	Mt Bogong	NSW	43	30	56	34	50	-	-
145	Heemskirk River	TAS	43	54	16	59	38	57	32
101	Yaouk Bill Range	ACT	44	40	42	33	-	-	61
108	Mt Black Jack	NSW	44	48	-	28	60	50	34
118	Bald Hill	NSW	44	28	-	39	-	51	59

* See Table 4 for key to sites.

TABLE 7—cont.

Provenance		Region	Average	Seedlot rankings on sites*					
No.	Origin			ROTO	LONGW	PILOT	MYRTL	TARRA	PARRA
154	Lake Tooms	TAS	46	59	20	53	45	48	50
115	Peppercorn Hill	NSW	47	45	—	38	56	56	39
150	Lake Pedder	TAS	47	45	44	57	43	45	48
147	Miena	TAS	50	57	54	52	44	45	45
114	Mt Flinders	NSW	50	52	50	40	49	53	56
136	Plateau Rd	TAS	53	49	—	57	—	—	—
155	Bicheno	TAS	53	58	—	61	53	42	51
146	King William Saddle	TAS	53	56	—	55	59	54	42
138	Ben Nevis	TAS	54	53	—	51	54	60	53
156	Fingal	TAS	57	61	—	58	57	61	49
137	Ben Lomond	TAS	59	62	60	60	61	59	54

* See Table 4 for key to sites.

The OP families (Sets 3 and 4), which were represented just at Rotoaira, varied widely in their rankings (Appendix 1). Of the top 10 seedlots (out of 144) at Rotoaira, three were from Tasmania, three from Victoria, and four were individual-family seedlots of New Zealand origin. Family-mean repeatability for diameter was 0.81 (Table 8). There was no discernible pattern of performance in relation to geographic source within New Zealand, some of the best- and worst-ranked families coming from the neighbouring Karioi and Rangataua Forests in central North Island. For stem straightness scores, very highly significant ($p < 0.001$) family differences (Table 8) translated into a family-mean repeatability of 0.77.

A feature of the New Zealand material was a high incidence of flowering. On average, flower abundance scores (details not shown) were double those of the native provenance lots.

TABLE 8—Analyses of variance for age-8 diameter and straightness score for New Zealand open-pollinated families at Rotoaira.

Item	Degrees of freedom	Diameter			Straightness		
		Mean square	F	P	Mean square	F	P
Reps	35	54.97	4.71	****	3.761	1.94	***
Sets	1	66.54	1.30†	NS	0.615	<1	NS
Reps × Sets	35	22.56	3.54	****	3.585	1.85	**
Families(sets)	44	33.74	5.30	****	8.298	4.28	****
Error	1160	6.368			1.941		
Family-mean heritability ($= (F - 1)/F$)			0.81			0.77	

NS p (probability > F under null hypotheses) > 0.05

** p < 0.01

*** p < 0.001

**** p < 0.0001

† Satterthwaite-type approximate test (SAS (SAS Institute 1989) PROC GLM, RANDOM statement, TEST option)

DISCUSSION

The outstanding feature of the results is the pattern of provenance rank changes between age-3 height and age-8 diameter. This was dominated by the general improvement of the

Tasmanian provenances relative to those from the mainland, such that there was no longer a clearly defined group of superior Victorian provenances (Table 7 and Appendix 1). The early recommendation of Wilcox (Forest Research Institute 1983, Wilcox *et al.* 1985), which was corroborated by the early Australian results (Moran *et al.* 1990), was in favour of Victorian provenances, but it must now be reviewed. It is possible that as the trees get older the growth performance of Tasmanian material relative to mainland provenances could improve still further.

Reasons for the turnarounds in provenance rankings are not clear. Despite some anecdotal reports (Wilcox, unpubl. data) there is no convincing evidence that differential defoliation by the beetle (*Paropsis charybdis*) or by leaf-spot fungi (*Mycosphaerella* spp.) have been decisive.

The tree-form difference, plus the apparently different growth curves, revealed by this study provide further evidence of differentiation between the mainland and Tasmanian subspecies. Greater heartwood formation in the mainland provenances (King *et al.* 1993) could have contributed, through diversion of resources into extractives at the expense of wood production (cf. Loehle & Namkoong 1987).

Such changes in comparative performance over time have been observed in provenance studies with other species. High-altitude sources of ponderosa pine (*Pinus ponderosa* P. et C. Lawson) showed slower growth than did mid-altitude sources at age 12, but at age 29 the latter were challenging the mid-altitude material for growth performance (Conkle 1973). Even more dramatic are some partially documented results with *P. muricata* D. Don. Early growth rates were fairly similar among provenances in a trial reported by Shelbourne *et al.* (1982), with no strong north-south trends, but since then most of the southern provenances have slowed down drastically, while the northern provenances have maintained their growth rates. Thus, depending on the species and test sites, early provenance trials results can be very misleading, and the trials may need to be monitored for much of the rotation.

For choice of provenance in *E. delegatensis*, tree form and wood properties may need to be considered in addition to growth rates. Tree form was statistically inferior in Tasmanian material, but the general standard of tree form was not a concern in the two New Zealand provenance trials. Form is more likely to be a concern for sawlog crops than for pulpwood, but the superior seasoning behaviour (i.e., less internal checking) of the wood of Tasmanian provenances (King *et al.* 1993) is likely to be a decisive consideration for sawn timber. The Tasmanian provenances admittedly suffered more wind damage in a runaway tropical cyclone (Forest Research Institute 1983) but that was an extreme climatic event, and wind damage does not usually rate as a limiting factor for *E. delegatensis*.

The average growth performance of the New Zealand material was disappointing. This may have reflected a predominance of NSW in the geographic origins, but other factors could have contributed. The abundant flowering could have caused a diversion of resources from stemwood production. That could well have reflected a response to unwitting selection for heavy and precocious seed production in an introduced species. An associated factor could have been inbreeding, since seed requirements can often be satisfied by felling a single, heavily laden tree, while the insect pollination would not be conducive to interpollination among scattered plantings of the sort that were often made. Founder effects and associated inbreeding depression could have depressed average growth and contributed to variation

among composite seedlots and families (cf. Burdon *et al.* 1992b). In fact, Seedlot No.73 (Crookston) is known to have a narrow genetic base. Overall, the situation may well have contrasted with that which tends to occur in conifer plantations, where a release from the neighbourhood inbreeding of natural stands is typically associated with increased vigour (e.g., Burdon *et al.* 1992a).

Differences among the New Zealand open-pollinated progenies were large. The exact causes of this variation are uncertain. Variation in provenance origins could well have contributed, although there is no clear evidence in support of this possibility. Differential effects of inbreeding could also have contributed in respect of diameter growth, as indicated earlier. In addition, founder effects could certainly have contributed. But even if only part of this family variation is additive genetic in nature, it could offer considerable scope for selection among families for genetic improvement. Whether that will be preferable to using native provenance material would depend on the advantages of Tasmanian material for longer-term growth rate (still uncertain) and for sawn timber (King *et al.* 1993), which both depend on the species being used for sawlog production.

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APPENDIX 1

Rankings of all 144 seedlots for age-8 diameter (DM08) at Rotoaira and Longwood, together with means for DM08, age-8 straightness (STR) and age-3 height (HT03). Only Set 1 was represented at Longwood, but all four sets were at Rotoaira.

No.	Provenance	Region	Average ranking	Rotoaira				Longwood			
				Rank* (m)	HT03 (mm)	DM08	STR	Rank* (m)	HT03 (mm)	DM08	STR
SET 1											
129	Mt Macedon	VIC	9	11	4.7	156	6.1	7	4.9	18.0	6.1
133	Mt Ewen	VIC	16	16	4.6	155	6.4	15	4.4	17.8	5.7
162	Mt Ellery	VIC	25	15	4.7	155	6.4	35	4.3	17.3	6.8
131	Mt Useful	VIC	30	10	4.5	158	6.5	50	3.9	17.2	6.5
135	Hartz Mts	TAS	31	42	4.1	148	4.5	19	4.3	17.8	5.1
142	Surrey Hills	TAS	39	38	4.2	149	4.1	39	4.2	17.3	3.8
147	Miena	TAS	49	70	3.5	142	4.3	27	3.4	17.5	4.3
150	Lake Pedder	TAS	49	50	4.0	146	4.6	47	3.8	17.3	5.7
137	Ben Lomond	TAS	52	17	3.2	154	5.1	86	3.0	16.7	4.8
132	Mt Skene	VIC	53	39	4.5	148	6.7	66	4.4	17.1	7.1
160	Bulls Head	ACT	54	97	4.0	136	6.4	11	4.0	18.0	6.0
171	Blue Range	VIC	55	56	4.6	145	6.8	54	4.4	17.2	6.1
161	Mt Delegate	NSW	60	62	4.2	143	6.5	58	3.6	17.1	7.1
151	Russell River	TAS	65	126	3.7	130	4.5	3	4.4	18.3	5.4
101	Yaouk Bill Range	ACT	68	58	4.0	144	6.7	78	3.8	16.7	5.8
163	Nunniong Plateau	VIC	69	33	4.2	150	6.9	105	3.9	16.3	6.0
124	Big Ben	VIC	70	117	4.3	132	6.0	23	4.1	17.6	5.9
141	Maggs Mt	TAS	71	98	4.1	136	5.4	43	4.0	17.3	4.9
116	Yarrangobilly	NSW	73	49	4.3	147	6.2	97	3.9	16.5	5.7
154	Lake Tooms	TAS	84	136	3.5	123	5.6	31	4.3	17.4	5.6
168	Kaingaroa	NZ	89	107	3.8	134	5.9	70	3.4	17.0	5.1
125	Razorback Spur	VIC	90	105	3.9	134	6.1	74	4.0	16.8	6.3
114	Mt Flinders	NSW	90	63	3.8	143	6.1	117	3.6	16.0	5.6
173	Rangataua	NZ	91	88	4.0	138	6.1	94	3.9	16.5	6.4
130	Ada River	VIC	93	85	4.9	139	6.4	101	4.4	16.3	7.1
145	Heemskirk River	TAS	94	79	3.7	141	4.8	109	4.3	16.2	4.5
110	Youngal	NSW	97	132	4.3	128	6.6	62	4.3	17.1	6.7
169	Bago SF	NSW	102	121	4.1	131	6.6	82	3.7	16.7	6.3
127	Royston River	VIC	106	78	4.8	141	5.3	133	4.0	15.1	7.0
122	Mt Buffalo	VIC	111	131	4.0	128	6.0	90	3.8	16.7	6.2
73	Crookston	NZ	118	114	4.1	133	6.2	121	3.8	15.8	6.9
119	Pilot Hill	NSW	120	127	3.9	129	6.9	113	4.0	16.1	7.1
104	Mt Bogong	NSW	122	102	4.2	135	6.7	141	3.4	15.1	6.0
112	The Pinnacle	NSW	124	110	4.1	134	6.2	137	3.4	15.1	6.5
174	Southland	NZ	125	125	3.9	130	6.8	125	3.9	15.7	6.5
126	Upper Howqua	VIC	135	140	4.5	120	7.0	129	3.7	15.6	6.6
SET 2											
157	Bendover Hill	TAS	2	2	4.4	165	5.0
164	Cromwell Knob	VIC	3	3	4.8	164	6.2
95	Karioi	NZ	13	13	4.4	156	6.7
103	Smokers Flat	ACT	14	14	4.4	156	6.4
167	Swifts Creek	VIC	18	18	4.6	154	6.5
102	Leura Gap	ACT	20	20	4.1	153	6.7
118	Bald Hill	NSW	22	22	4.2	152	6.0
109	Cascade	NSW	23	23	4.5	152	6.3
144	Luina	TAS	26	26	4.4	152	5.6

* Rankings all rescaled to 1–144 (SAS [SAS Institute 1989] PROC RANK, TIES = HIGH)

APPENDIX 1—cont.

No.	Provenance	Region	Average ranking	Rotoaira			Longwood				
				Rank*	HT03	DM08	STR	Rank*	HT03	DM08	STR
158	Mt Gibbo	VIC	28	28	4.5	152	6.5
35	Maggs Mt	TAS	31	31	4.0	150	5.2
159	Forlorn Hope Tk	VIC	34	34	4.1	149	6.8
33	Fingal	TAS	35	35	3.4	149	6.1
32	Fingal	TAS	53	53	3.6	145	5.0
156	Fingal	TAS	55	55	3.3	145	5.2
17	Mt Margeret	VIC	60	60	4.0	144	7.2
136	Plateau Rd	TAS	61	61	3.9	144	3.8
9	West King	VIC	71	71	4.3	142	6.5
120	Mt Wills	VIC	74	74	4.7	142	6.4
26	Collinsvale	TAS	77	77	3.6	142	5.7
139	Dazzler Range	TAS	82	82	4.1	140	5.4
106	The Granites	NSW	87	87	4.0	139	6.6
108	Mt Black Jack	NSW	90	90	3.9	138	6.2
36	Great Lake	TAS	93	93	3.5	138	3.5
111	Geehi	NSW	94	94	4.7	138	6.6
165	Royston River	VIC	103	103	5.2	135	6.8
105	Clear Ck	NSW	104	104	4.3	134	6.7
42	Golden Downs	NZ	112	112	3.9	133	6.9
172	Rowallan	NZ	115	115	4.1	133	6.9
14	Currajong Ck	VIC	122	122	4.5	131	6.4
113	Dargals Range	NSW	123	123	4.4	130	6.0
37	Snowy Mts	NSW	128	128	3.8	129	7.0
31	Bondo S.F.	NSW	129	129	3.6	129	6.0
107	Mt Nurenmeremang	NSW	133	133	4.0	127	6.4
12	Bindaree	VIC	137	137	4.5	123	6.6
41	Taranna	TAS	144	144	4.0	101	6.0
SET 3											
38	Ben Nevis	TAS	1	1	3.9	170	5.2
85	Kaingaroa	NZ	5	5	4.1	160	6.9
134	Mt Baldhead	VIC	7	7	4.5	159	6.5
148	Tunbridge Tier	TAS	8	8	3.9	158	4.4
56	Golden Downs	NZ	9	9	4.2	158	6.3
40	Mt Nunniong	VIC	12	12	4.8	156	6.5
117	Gungarlin River	NSW	19	19	4.4	153	6.3
8	King River	VIC	21	21	4.8	153	6.6
18	Connors Plain	VIC	24	24	4.7	152	7.0
146	King William Saddle	TAS	28	28	3.6	152	5.7
143	Yellow March Rd	TAS	29	29	4.1	151	4.6
128	Lake Mountain	VIC	30	30	4.8	150	7.2
21	Upper Thompson Riv	VIC	36	36	4.8	149	6.5
39	Misery Plateau	TAS	37	37	4.3	149	5.1
149	Mt Dromedary	TAS	42	42	4.1	148	5.0
19	Omeo	VIC	43	43	4.5	148	6.9
65	Longwood	NZ	46	46	4.3	147	7.6
153	Middle Peak	TAS	47	47	4.2	147	4.8
138	Ben Nevis	TAS	48	48	3.8	147	5.8
93	Kaingaroa	NZ	52	52	4.2	146	6.2
47	Rangiwahia	NZ	59	59	2.6	144	6.5
121	Beecher Hill	VIC	64	64	4.5	143	6.1
48	Rangataua	NZ	65	65	4.5	143	6.4
10	King Saddle	VIC	66	66	4.6	143	6.7

* Rankings all rescaled to 1–144 (SAS [SAS Institute 1989] PROC RANK, TIES = HIGH)

APPENDIX 1—cont.

No.	Provenance	Region	Average ranking	Rotoaira			Longwood				
				Rank* (m)	HT03 (mm)	DM08	STR	Rank* (m)	HT03 (mm)	DM08	STR
115	Peppercorn Hill	NSW	67	67	4.0	143	6.5
55	Golden Downs	NZ	69	69	4.1	142	7.5
140	Cluan Tier	TAS	75	75	3.4	142	5.4
155	Bicheno	TAS	80	80	3.5	140	6.8
11	Mansfield	VIC	83	83	4.3	139	6.2
16	Mt Wills	VIC	86	86	4.5	139	6.9
34	Patersonia	TAS	89	89	3.8	138	5.7
69	Brooksdale	NZ	95	95	4.2	137	7.2
94	Kaingaroa	NZ	99	99	4.0	135	6.8
13	Mansfield	VIC	106	106	4.4	134	6.2
123	Big Hill	VIC	111	111	4.8	133	6.1
57	Taurewa	NZ	134	134	3.7	126	6.1
SET 4											
46	Rangataua	NZ	4	4	4.3	162	7.1
4	Karioi HQ	NZ	6	6	4.3	159	6.6
89	Karioi	NZ	26	26	4.5	152	7.6
28	Golden Downs	NZ	32	32	4.1	150	7.3
70	Moa Flat	NZ	40	40	4.2	148	7.4
86	Karioi	NZ	44	44	4.8	148	6.6
5	Karioi HQ	NZ	45	45	4.3	147	5.9
88	Karioi	NZ	51	51	4.4	146	6.4
52	Whirinaki	NZ	54	54	4.4	145	6.3
58	Rangataua	NZ	57	57	4.2	145	7.0
59	Rowallan	NZ	68	68	4.2	142	6.9
6	Te Awa	NZ	72	72	4.3	142	7.3
90	Karioi	NZ	73	73	4.2	142	7.6
66	Longwood	NZ	76	76	3.9	142	7.4
60	Rowallan	NZ	81	81	4.0	140	6.4
87	Karioi	NZ	84	84	4.0	139	7.1
91	Karioi	NZ	91	91	4.6	138	7.3
63	Longwood	NZ	92	92	4.4	138	6.5
67	Longwood	NZ	96	96	3.6	136	6.9
51	Whirinaki	NZ	100	100	4.3	135	7.3
71	Moa Flat	NZ	101	101	3.9	135	6.1
3	Karioi HQ	NZ	108	108	4.0	134	6.8
7	Rangataua	NZ	109	109	3.6	134	6.7
61	Rowallan	NZ	113	113	3.7	133	7.3
64	Longwood	NZ	116	116	3.9	132	6.8
1	Te Awa	NZ	118	118	3.8	131	7.5
2	Karioi	NZ	119	119	4.1	131	7.2
49	Whirinaki	NZ	120	120	4.2	131	6.5
92	Karioi	NZ	124	124	4.2	130	6.9
62	Longwood	NZ	130	130	3.7	129	6.4
53	Whirinaki	NZ	135	135	3.9	124	6.6
68	Longwood	NZ	138	138	3.9	121	7.4
72	Moa Flat	NZ	139	139	3.6	121	7.1
45	Rangataua	NZ	141	141	4.2	120	5.7
50	Whirinaki	NZ	142	142	4.1	119	5.8
54	Whirinaki	NZ	143	143	3.6	110	5.8

* Rankings all rescaled to 1–144 (SAS [SAS Institute 1989] PROC RANK, TIES = HIGH)