PROVENANCE VARIATION, GENOTYPE BY ENVIRONMENT INTERACTIONS AND AGE-AGE CORRELATIONS FOR *EUCALYPTUS REGNANS* ON NINE SITES IN SOUTH EASTERN AUSTRALIA

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ABSTRACT

Forty-nine provenances from a rangewide collection of *Eucalyptus regnans* F. Muell were established at each of 12 sites throughout its natural distribution. Trees on the nine surviving sites were assessed for diameter at breast height, stem straightness and branching quality at ages between 9 and 13 years.

Provenance differences were found at each site but genotype by environment interactions were also significant. Provenance rankings differed between sites and no single provenance or group of provenances was found to be among the best for all traits at all sites. Several provenances (Mt Useful, Quarry Creek, Buchan, Otway Messmate and New Haven) were consistently amongst the worst for growth at all sites. For stem straightness Narbethong was outstanding, ranking highly across all sites, whereas Lavers Hill, Christmas Hills and Strathblane were consistently amongst the worst. Local provenances did not perform amongst the best at eight out of the nine sites. Provenance differences did not appear to follow any systematic pattern and no geographic grouping of provenances appears possible. Based on mean performance across all sites the best provenances for diameter growth were Mirboo East and Gunyah from Gippsland, Victoria and Forester and Gould's Country from Tasmania.

Three assumptions underlying the design of provenance testing strategies are examined: that large provenance differences are expected, that these differences are expected to show some pattern and that provenances may be grouped into geographic areas. These assumptions were not found to be valid for this study. No large provenance differences were found and no consistent patterns of performance across sites were evident. Two options were considered for forming a breeding population for this species: selecting provenances that perform reasonably well across many sites or making the assumption that each provenance will contain good families and include a broad geographic range of material.

Key words: Eucalyptus regnans, provenance variation, G × E interactions, age-age correlations

INTRODUCTION

When developing a strategy for a breeding program the choice of seed sources for inclusion in the initial breeding population is critical as the constitution of this population will have an over-riding effect on the programs future progress. Choice of seed sources must be based on knowledge of the natural patterns of variation within the species, the range of potential planting sites and the potential for genotype by environment interactions. This information is used, together with the breeding objectives of the program, to identify the optimal mixture of seed sources for the breeding population(s) (RAYMOND 1989). Breeding programs for *Eucalyptus regnans* F. Muell were initiated in the 1970s, coinciding with the establishment of plantations in both south-eastern Australia and New Zealand (WILCOX *et al.* 1980, WILCOX 1982, CAMERON & KUBE 1983). *E. regnans* occurs naturally in the south-eastern Australian states of Victoria and Tasmania. It is a fast-growing species which is intolerant of severe cold or drought and its natural distribution is thus discontinuous, as it is restricted to temperate, moist sites with deep soils (GRIFFIN *et al.* 1982). *E. regnans* produces high quality sawn timber suitable for joinery, furniture and construction and high quality pulp and paper from both chemical and mechanical pulping processes. Commer cial plantations of *E. reg-* *nans* in Australia are established for pulpwood and, to a minor extent, sawlogs. Tree characteristics desired to meet these objectives are adaptation to a range of sites, rapid growth, straight stems and fine branches which shed easily.

From trials in Victoria, ELDRIDGE (1968, 1971, 1972) determined that considerable genetic variation existed both within and between populations for traits including growth rate, stem straightness, branching, flowering, survival and frost tolerance. Attempts were made to group provenances based on observed patterns of variation by both CHAPPILL (1983) and WILCOX (1982). Chappill studied capsule morphology for 20 provenances collected by GRIFFIN (1983a) and found geographic differences, with Tasmanian capsules being generally larger although the range of variation between provenances from Tasmania and Victoria overlapped considerably. Provenances were grouped into 5 geographic areas (high altitude Victoria, low altitude Victoria, coastal Victoria plus north coast Tasmania, east plus south coastal Tasmania and inland Tasmania) which were significantly different from each other for capsule traits. Seedling and sapling morphological traits were studied in 6 provenances which are also included in the current study (Powelltown, Valencia Creek, Upper Ford River, New Haven, Murdunna and Strathblane) plus Otway Messmate. For seedling traits only Otway Messmate was distinct from the other populations which could not be differentiated and were not found to follow any geographic grouping. However, for sapling traits the discrimination of the populations was good with increasing leaf length, width, area and petiole length found to be highly correlated to decreasing altitude, distance to sea or latitude. Chappill concluded that the three morphological data sets could each be related to aspects of the environment but the aspects of the environment showing the best correlations differed for each data set.

WILCOX (1982) grouped *E. regnans* provenances into geographic areas based on growth at age three from two trials in New Zealand's north island. Of the 36 provenances in Wilcox's study 27 provenances were common to the current study. Trees were assessed for height, disease susceptibility (fungal leaf blotch attributed to *Mycosphaerella cryptica* (Cke) Hansf.), branch quality and stem straightness. From these results Wilcox proposed grouping the Australian provenances into 6 geographic groups: high elevation Victoria (>900 m), central Victoria, south Gippsland and Otway Ranges, interior south Tasmania, coastal east and south-east Tasmania and northern Tasmania.

A two-stage breeding strategy for *E. regnans* was proposed by GRIFFIN (1983a) with extensive range -wide provenance testing of bulked seedlots in Stage 1

followed by establishment of progeny trials for the top 20% of provenances in Stage 2. Selection of provenances for Stage 2 would be based on fifth-year growth data from the Stage 1 provenance trials. For Stage 1, twelve provenance trials were established during 1977/78. Provenance seedlots were collected from throughout the natural distribution of the species and established on five sites in Victoria and seven sites in Tasmania. Objectives for these Stage 1 trials (GRIFFIN 1983a) were firstly to determine the best natural seed sources for planting in Victoria and Tasmania and secondly to assess the extent of interactions between provenance and planting sites. Details of the seed collections, selection of sites, trial design, nursery results and field performance at one year of age were given in GRIFFIN et al. (1982).

Of the 12 trials planted initially by GRIFFIN for Stage 1 of the breeding strategy, only nine remained suitable for assessment at age 10. Each of these remaining sites was assessed for height and diameter growth, stem form and branching quality. Results for within site analyses of diameter, survival, stem straightness and branch quality are presented in this paper. Complete results for other traits assessed, including height, plot volume and stem defect counts are available in RAY-MOND and VOLKER (1994). Across site genotype by environment analyses are also reported for diameter and survival and the suggested groupings of provenances are re-evaluated. In addition, results for height and frost damage assessed at age one in the same trials (GRIFFIN et al. 1982) were used to calculate correlations with later age diameter and survival.

MATERIALS AND METHODS

Trial design

Each trial was established as a 7×7 balanced lattice or lattice square containing 49 provenances. Fifty-two provenances in total were planted with 46 of these being planted on all sites. Locations of provenances and sites are shown on Figure 1, details for each provenance are presented in Table 1 and site details are given in Table 2. At the Victorian sites one of the provenances (13, Mt Erica 990m) was duplicated and is also listed as provenance 16. For the Tasmanian sites, with the exception of Deloraine, an additional provenance (50, Gunyah, was included). Seedlings planted at the Deloraine site in 1977 failed and this site was replanted in 1978 with two additional provenances included to replace provenances 17 and 50. These two provenances (51 Mawbanna and 52 Lavers Hill) were both E. obliqua and not E. regnans and were not included at any other site. Provenance 26, Otway

Prove	nance		Latitude	Longitude	Altitude		
1	Mt Disappointment	VIC	37° 25'	145° 12'	640	52	11
2	Kallista	VIC	37° 55'	145° 23'	245-365	28	13
3	Toolangi	VIC	37° 31'	145° 31'	720-780	61	16
4	Narbethong	VIC	37° 31'	145° 38'	600-800	70	55
5	Armstrongs Creek	VIC	37° 36'	145° 49'	640-760	83	11
6	Powelltown	VIC	37° 47'	145° 49'	760-820	56	14
7	Tarago	VIC	37° 56'	145° 55'	360-600	51	16
8	Rubicon	VIC	37° 20'	145° 56'	550-560	100	13
9	Mt Toorongo Track	VIC	37° 48'	146° 07'	1000	84	14
10	Barkly River	VIC	37° 27'	146° 29'	650-750	112	11
11	Mt Useful	VIC	37° 41'	146° 32'	910-990	95	15
12	Mt Erica 490m	VIC	37° 55'	146° 22'	490	95	
13	Mt Erica 990m	VIC	37° 54'	146° 24'	990	95	7
14	Valencia Creek	VIC	37° 33'	147° 00'	975	78	13
15	Quarry Creek	VIC	37° 26'	147° 39'	700-800	66	50
16	Mt Erica 990m	VIC	37° 54'	146° 24'	990	95	7
17	Buchan	VIC	37° 14'	148° 03'	600-800	66	10
18	Yalmy River	VIC	37° 21'	148° 27'	825	48	12
19	Bendoc	VIC	37° 18'	148° 58'	1040-1080	64	10
20	Narracan	VIC	38° 15'	146° 13'	300	46	14
21	Wilsons Promontory	VIC	39° 06'	146° 22'	370-400	3	11
22	Mirboo East	VIC	38° 31'	146° 23'	300-360	24	18
23	Traralgon Creek	VIC	38° 26'	146° 31'	550-600	45	50
24	Carisbrook	VIC	38° 36'	143° 45'	365-490	8	11
25	Upper Ford River	VIC	38° 39'	143° 29'	335-395	12	14
26 ^A	Otway Messmate	VIC	38° 36'	143° 39'	400	15	Bulk
27	New Haven	TAS	41° 01'	145° 22'	240	25	3
28	Ferndene	TAS	41° 09'	146° 01'	180-220	10	11
29	Lorinna	TAS	41° 35'	146° 05'	450-500	46	11
30	Christmas Hills	TAS	41° 28'	146° 36'	335	34	11
31	Beaconsfield	TAS	41° 18'	146° 45'	335-465	21	15
32	Lisle	TAS	41° 15'	147° 22'	580-600	29	15
33	Ben Nevis	TAS	41° 25'	147° 33'	250-300	44	10
34	Forester	TAS	41° 05'	147° 46'	200	22	12
35	Dans Valley	TAS	41° 23'	147° 53'	440-460	39	15
36	Royal George	TAS	41° 56'	147° 56'	620	30	11
37	Goulds Country	TAS	41° 13'	148° 09'	150	11	13
38	Florentine Valley	TAS	42° 29'	146° 27'	360-380	80	15
39	Styx	TAS	42° 49'	146° 36'	340-520	56	15
40	Moogara	TAS	42° 47'	146° 54'	600-700	28	11
41	Strathblane	TAS	43° 22'	146° 58'	200-280	5	12
42	Stoneyhurst Creek	TAS	42° 40'	147° 04'	450-460	39	10
43	Kaoota	TAS	43° 01'	147° 09'	480-500	8	12
44	Fern Tree	TAS	42° 55'	147° 15'	320-500	6	7
45	Bruny Island	TAS	43° 24'	147° 16'	260-280	4	12
46	Levendale	TAS	42° 31'	147° 32'	150	25	13
47	Nugent	TAS	42° 42'	147° 49'	340-400	11	13
48	Swan Port	TAS	42° 24'	147° 51'	420-480	12	11
49	Murdunna	TAS	42° 58'	147° 57'	350	5	12
50	Gunyah	VIC	38° 31'	148° 23'	300-360	24	4
51 ^в	Mawbanna	TAS	40° 55'	145° 21'	90	12	Bulk
52 ^в	Lavers Hill	VIC	38° 40'	143° 21'	270	13	11

Table 1 Provenance location information for E. regnans provenance study

messmate, is a naturally occurring hybrid of *E. regnans* x *E. obliqua* (GRIFFIN & ELDRIDGE 1980).

For each planting site a "local" provenance has been defined as the one having the closest geographic

<u></u>	<u> </u>	<u> </u>	Site		
	Browntown Rd Otway Ranges	Linkleterrs Rd Strzelecki Ranges	Toolangi	Geeveston	Upper Naton
Latitude	38° 38'	38° 27'	37° 31'	43° 12'	41° 11'
Longitude	143° 31'	146° 28'	145° 33'	146° 56'	145° 53'
Elevation (m)	520	500	770	120	320
Distance from ocean(km)	16	42	60	5	13
Soil type	Duplex soil loamy texture over yellow clay	Clay loam over weathered sandstone	Brown friable porous eart	Shallow sandy soil over gravelly B horizon	Red-brown clay Ioam
Cooperating organisation	Center for Forest Tree Technology Vicotria	Amcor Plantations Pty Ltd	Center for Forest Tree Technology Vicotria	Australian Paper Manufacturers Ltd.	North Eucalypt Technologies
Age at assessment	13	12	12	12	12
Design	Lattice	Lattice	Lattice	Lattice	Lattice
No of replicates	8	8	8	8	8
No of trees per plot	9	9	9	9	9
Mean DBH (cm)	18.80	18.98	21.12	10.18	14.50
Mean height (m)	20.47	19.58	23.64	11.03	14.16
Mean survival	49.6	53.3	48.9	73.3	68.0

Table 2. Site and experimental design details for the nine surviving E. regnans provenance trials

			Site	
	Woolnorth	Deloraine	Lone Star Scottsdale	Womerah Rd Strzelecki Ranges
Latitude	40° 48'	41° 36'	41° 12'	38° 28'
Longitude	144° 54'	146° 41'	14/~ 18'	146° 30'
Distance from ocean(km)	5	50	23	425 27
Soil type	Yellow friable earth	Sandy soil	Very friable light sandy soil	Clay loam over weathered sandstone
Cooperating organisation	North Eucalypt Technologies	North Eucalypt Technologies	Forestry Tasmania	Centre for Forest Tree Technology, Victoria
Age at assessment	10	9	10	12
Design	Lattice	Lattice	Lattice Square	Lattice Square
No of replicates	8	8	4	4
No of trees per plot	9	9	30	30
Mean DBH (cm)	15.82	7.35	11.87	20.14
Mean height (m)	11.76	7.80	10.30	20.80
Mean survival	73.1	55.5	31.2	65.2



Figure 1. Distribution of provenances of Eucalyptus regnans

origin to the site based on latitude, longitude and altitude information from Tables 1 and 2.

Of the 12 trials established (GRIFFIN *et al.* 1982) only 9 survived to age 10 and were available for assessment. Seven trials (see Table 2) were established as balanced lattices with 8 replicates of 9 tree plots. The remaining 2 trials were established as balanced lattice squares with 4 replicates of 30 tree plots planted as a 5 x 6 rectangle.

Trial assessment at ages 9 to 13 years

Diameter over bark at 1.3m (DBH) was measured on all trees at all sites. For each site, except Womerah Rd, the following characters were assessed on all trees:

- stem straightness (STR) using a 6 point score with 6 being the best and 1 being the worst (see RAY-MOND & COTTERILL 1990 for details)
- branch quality (BRN) also using a 6 point scale

Data analyses within sites

All dead or missing trees were treated as missing values for DBH, STR and BRN. Prior to analysis, individual tree data were converted to either plot means or totals and the following variates analysed:

- mean DBH (cm) for each plot (DBH)
- * percentage survival for each plot (SURVIVAL)
- mean straightness score (STR)
- * mean branching score (BRN)

In order to stabilise the variances an arc sine transformation was applied to the data for SURVIVAL prior to analysis.

Provenance means for each trait at each site were estimated fitting the following model to the lattice design using Residual Maximum Likelihood (REML) with replicates and provenances considered to be fixed effects and incomplete blocks within replicates considered to be random and independent of the error term.

$$Y_{ijk} = \mu + R_i + B_{ij} + P_k + e_{ijk}$$

where : Y_{ijk} – mean or total for each plot; μ – overall mean; R_i – effect of replicate i; B_{ij} – effect of the jth incomplete block within the ith replicate; P_k – effect of provenance k; e_{ijk} – residual.

For the two sites planted as balanced lattice squares a similar model was fitted with the incomplete block term being replaced by row within replicate and column within replicate terms. Both rows and columns within replicates were considered to be random effects.

The provenance means obtained from REML by fitting the above model are Best Linear Unbiased Estimators (BLUEs) adjusted for incomplete block effects.

Correlations between sites

For comparison of different traits across sites correlations between provenance means for DBH, STR and BRN were calculated between all pairs of sites.

Genotype by environment interaction

For the G × E analyses several provenances (16, 50, 51 and 52) were excluded on the basis that they had been planted on too few sites. The other provenance excluded was 26 (Otway Messmate) as this is not true *E. regnans* but an intermediate between *E. obliqua* and *E. regnans* (GRIFFIN & ELDRIDGE 1980).

To determine whether provenance mean diameter was dependent upon survival the correlations between DBH and SURV for each site were calculated. These correlations were low and non-significant indicating that the reduced levels of within-plot competition resulting from lower survival did not produce larger trees. Across-site analyses of DBH could thus be conducted without the DBH data requiring adjustment for differential survival.

Data were then analysed across sites in several

ways. Firstly, the significance of the provenance by site interaction was evaluated using a two stage analysis of variance. The two way tables of mean diameter and survival for each provenance at each site were used to evaluate the significance of site and provenance effects, fitting the following general linear model with all effects considered to be fixed:

$$Y_{ij} = \mu + P_i + S_j + e_{ij}$$

where: Y_{ij} – estimated mean diameter for Provenance i at Site j; μ – overall mean; P_i – effect of Provenance i; S_i – effect of Site j; e_{ij} – residual.

As the residual term from the above analysis is actually the site x provenance interaction term a weighted pooled plot residual was calculated as follows: the residual mean square for each site was divided by the number of replicates for that site, these terms were then summed and the total divided by the number of sites (WILLIAMS & MATHESON 1994, Chapter 5). This pooled residual was then used to determine the significance of the provenance by site interaction term.

Secondly, joint regression analysis (FINLAY & WILKIN-SON 1963) of a two-way table of provenance means at each site for DBH was used to investigate the nature of the observed provenance by site interaction. The model fitted was:

$$Y_{ij} = \mu + P_i + g_i \cdot S_j + e_{ij}$$

where the g_i are the regression parameters for provenances which reflect the different behaviour of provenances across sites. As not all provenances were established at all sites the two-way table was incomplete thus the sequential analysis mapped out by FINL-AY & WILKINSON, where P_i and S_j are estimated first followed by g_i , is only approximate. The simultaneous analysis method presented by DIGBY (1979) and as described in WILLIAMS & MATHESON (1994) was thus used. Results of these analyses are usually presented in graphical form (with g_i plotted against P_i).

To determine whether provenances could be grouped geographically, a range of analyses including canonical correlation, alternative clustering analyses and regression of provenance means against latitude and altitude of origin were explored. None of these analyses were successful in providing any grouping of provenances that could be interpreted in any sensible geographic or biological manner.

The groupings of provenances suggested by CHAP-PILL (1983) and WILCOX (1982) were evaluated by reanalysing the data with a range of additional terms included in the model. Firstly, Model 2 above was refitted including a term for state of origin of the provenances (Victoria or Tasmania) with provenances nested within state. Secondly, to evaluate CHAPPILL (1983) groupings which were based on morphological traits, the data set was reduced to include only provenances common to both studies and the model fitted included terms for site, group and provenance within group. Finally, WILCOX's (1982) groupings were evaluated. The classification based on the New Zealand results was extended to cover all provenances in the current study and an additional group added to cover the outlying populations in eastern Victoria which were not included in his study. The geographic groupings and allocation of provenances are as follows:

- High elevation (>900 m altitude) central Victoria 9, 13
- 2) Central Victoria 1, 2, 3, 4, 5, 6, 7, 8, 12
- South Gippsland and Otways 20, 21, 22, 23, 24, 25, 50
- Eastern Victoria outlying provenances 10, 11, 14, 15, 17, 18, 19
- 5) Coastal eastern and south-eastern Tasmania 36, 41, 43, 44, 45, 46, 47, 48, 49
- 6) Northern Tasmania 27, 28, 29, 30, 31, 32, 33, 34, 35, 37
- Interior southern Tasmania (>420 m altitude) 38, 39, 40, 42

The following model was then fitted with all effects considered to be fixed:

$$Y_{ijk} = \mu + S_i + G_j + P_{jk} + SG_{ij} + e_{ijk}$$

where: Y_{ijk} – estimated mean diameter for Provenance k in Group j at Site i; μ – overall mean; S_i – effect of Site i; G_j – effect of Group j; P_{jk} – effect of Provenance k within Group j; SG_{ij} – interaction between Sites and Groups; e_{ijk} – residual.

As the residual term from the above analysis is actually the site \times provenance interaction term, the weighted pooled plot residual calculated above was used to test the significance of this term.

Finally, correlations between early data reported by GRIFFIN *et al.* (1983) and the current data were estimated as follows: simple correlations of provenance means at each site for DBH with height growth at age 1 (HT-1) and SURV with frost damage score at age 1 (FROST-1)

RESULTS

Within site analyses

Provenance means (BLUEs) for DBH, SURVIVAL, STR and BRN are presented in Tables 3 to 6 respectively. Data for the local provenances at each site are

Deer	BRC	WN	LIN	١K	ТО	OL	GEE	EVE	NAT	ON	WOO	DLN	DEL	OR	LO	NE	WON	ЛER
	DBH	R	DBH	R	DBH	R	DBH	R	DBH	R	DBH	R	DBH	R	DBH	R	DBH	R
1	20.1	14	21.3	7	22.8	8	10.3	26	15.3	18	17.1	8	7.7	17	11.3	32	20.9	16
2	18.2	28	16.6	45	22.0	13	10.3	23	16.9	6	15.2	31	7.4	22	12.7	15	17.9	48
3	19.3	18	17.4	42	22.5	9	10.6	18	16.6	7	16.2	20	8.2	10	11.7	29	20.6	19
4	17.0	41	18.1	32	21.5	19	10.5	20	14.3	26	14.9	35	8.2	8	11.9	24	19.5	33
5	16.8	42	18.4	30	23.4	4	8.9	41	13.9	34	14.7	40	6.7	39	11.7	28	19.4	37
6	19.9	16	17.9	35	20.8	9	10.9	16	14.2	28	16.8	12	6.7	37	11.4	31	20.0	27
7	17.3	39	21.6	4	23.7	3	10.7	17	17.4	3	16.0	23	7.2	26	11.8	26	21.7	3
8	16.3	47	17.6	40	20.6	33	10.5	19	14.2	30	13.6	44	6.4	43	10.8	37	19.7	32
9	18.5	27	17.5	41	21.8	16	10.1	28	12.9	42	13.3	47	6.7	38	9.4	48	18.6	45
10	17.8	33	20.4	12	20.8	27	11.2	13	14.2	29	14.7	39	6.0	45	12.2	17	19.4	36
11	14./	49	10.5	40	20.5	34 6	9.0	40	14.7	24	13.3	45	7.1	31	9.3	49	18.7	41
12	20.0	15	20.3	10	23.2	19	11.2	12	1/.0	2	16.0	24	10.0	1	12.9	14	20.8	18
14	18.2	20	180	22	21.5	10	10.5	21	14.8	23 47	10.0	21	7.2	28	9.9	40	21.6	20
15	173	40	18.5	26	19.1	30 46	9.9	22	12.0	47	13.2	33 46	1.5	24 41	10.8	38 42	19.9	30
16	18.1	31	17.7	39	20.6	32	9.7	55	15.1	40	13.5	40	0.5	41	10.4	43	19.2	39 17
17	14.9	48	17.8	37	19.8	41	85	46	133	37	12.9	48			10.1	15	20.0	17
18	17.6	36	16.9	43	20.1	39	8.8	42	13.6	35	15.5	28	75	19	10.1	36	10.0	31
19	19.1	21	18.7	25	19.7	42	10.2	27	14.4	25	14.6	41	7.8	13	96	47	21.2	10
20	19.2	19	18.8	24	22.3	12	11.6	6	16.0	11	16.5	16	7.7	16	11.4	30	22.4	2
21	21.4	6	22.4	2	22.0	14	9.4	35	15.5	15	18.7	3	7.3	25	11.9	25	21.5	7
22	22.0	3	19.0	21	24.8	1	11.5	7	17.0	4	17.5	7	8.7	6	14.4	1	20.1	25
23	21.7	4	20.5	10	23.3	5	11.7	4	14.3	27	16.4	17	7.6	18	13.0	11	22.8	1
24	23.4	1	18.9	23	23.1	7	9.1	39	12.2	46	16.7	14	6.1	44	11.0	34	18.6	46
25	20.5	10	20.4	11	22.4	11	8.5	45	15.5	16	14.6	42	5.5	48	11.9	23	20.9	14
26	16.3	46	18.1	33	15.2	49	10.3	22	8.4	49	12.0	49	5.8	47	13.7	7	17.4	49
27	19.8	17	16.9	44	19.6	43	8.0	48	9.0	48	15.3	29	5.2	49	12.0	21	21.2	9
28	16.7	44	20.0	17	20.2	37	12.4	3	14.0	32	17.0	9	7.5	20	13.9	4	21.1	12
29	16.8	43	20.5	9	20.3	35	9.3	36	15.0	21	15.2	32	6.9	34	11.3	33	20.3	24
30	17.6	37	16.0	47	18.9	47	9.1	38	13.3	38	16.7	13	6.4	42	12.0	20	19.5	34
31	18.7	25	21.7	3	22.0	15	11.4	9	15.6	14	18.0	5	6.6	40	13.4	9	20.9	13
32	18.7	24	18.6	28	20.8	26	11.3	11	16.3	8	16.9	11	7.2	29	13.7	8	20.0	28
22	20.1	13	20.4	13	20.8	28	11.4	8	15.2	19	17.7	6	8.1	11	13.4	10	20.4	23
34 25	22.4	22	20.7	0 16	24.1	10	10.0	30	15.0	13	19.5	2	9.3	3	13.8	2	21.4	8
36	20.1	12	17.8	28	22.5	21	12.9	1	10.2	9	17.0	10	9.4	2	13./	0	20.5	22
37	20.1	7	23.2	1	21.4	21	10.0	49	12.7	44	10.0	22 A	0.0	40 27	10.5	41	19.5	38
38	18 1	30	18.3	31	21.5	17	12.9	2	16.0	10	15.0	25	8.0	12	14.5	2	21.7	4
39	20.6	8	20.1	15	20.7	30	9.5	34	12.9	43	15.5	27	82	9	11.1	27	19.9	29
40	20.2	11	19.0	20	21.3	23	11.1	14	15.7	12	15.8	26	6.9	33	13.0	12	21.2	11
41	21.5	5	17.9	36	21.4	22	9.2	37	15.2	20	15.1	34	6.8	35	12.4	16	21.5	6
42	17.8	35	15.9	48	19.2	45	10.3	25	13.2	39	14.3	43	7.2	30	10.5	42	18.6	42
43	17.4	38	15.4	49	20.7	31	8.8	43	13.4	36	14.8	38	7.8	14	12.1	18	18.6	43
44	17.8	34	21.4	5	19.4	44	10.0	29	13.9	33	14.8	37	6.9	32	10.7	39	20.0	26
45	19.0	22	18.5	29	18.6	48	8.7	44	14.1	31	16.3	19	8.3	7	10.4	44	20.6	20
46	18.9	23	18.0	34	21.2	25	11.6	5	14.9	22	14.8	36	8.9	4	12.1	19	18.4	47
47	19.1	20	19.1	19	19.8	40	9.8	32	12.3	45	15.3	30	6.8	36	11.0	35	19.4	35
48	20.6	9	21.4	6	21.4	20	10.3	24	15.5	17	16.5	5	7.7	15	10.7	40	20.6	21
49	16.4	45	18.6	27	20.2	38	8.2	47	13.1	41	16.4	18	7.4	21	11.9	22	19.1	40
50							11.3	10	16.9	5	19.6	1	- -	•	12.9	13		
51													7.3	23				
52													8.8	5				
mean	18.8		19.0		21.1		10.2		14 5		15.8		73		11.0	_	20.1	-
s.e.	1.66		1.6		1.08		1.07		1.27		1.04		1.08		1.12		1 28	

Table 3. Mean diameter at 1.3 m over bark (DBH, cm) for each *E. regnans* provenance at each site together with rankings (R). Local provenance at each site marked by bold.

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Drov	BRO	WN	LIN	IK	TOC	DL	GEE	VE	NAT	ON	woo	DLN	DEL	OR	LON	VE	WON	1ER
	SURV	R	SURV	R	SURV	R	SURV	R	SURV	R	SURV	R	SURV	R	SURV	R	SURV	R
1	49	23	64	10	54	21	76	21	61	37	63	38	59	19	27	42	66	20
2	35	47	36	47	60	11	70	32	68	28	79	14	48	36	31	26	65	28
3	56	15	48	31	61	10	83	7	73	14	76	21	72	5	33	20	60	39
4	60	12	51	26	66	2	72	28	65	32	76	20	57	22	29	31	71	12
5	63	9	49	30	55	17	81	10	70	25	62	40	59	20	29	32	66	22
6	54	18	47	33	67	1	71	30	66	30	84	8	62	14	34	14	75	5
7	46	30	51	27	66	4	82	9	61	36	65	34	72	4	28	35	67	17
8	22	17	52	24	45	30	77	18	76	10	74	24	51	31	22	48	59	41
9	61	10	69 40	6	52 29	23	54	4/	61	38	56 92	4/	62 50	13	34	13	74	6
10	20	11	40	44	38	41	70	· 31	93	1	83	20	50	34	29	30	13	8
12	39	41	40	13	54	45	80	11	70	23	/1	50	01	10	20	49	00 51	23 47
12	40 56	16	40 76	45	53	22	80 74	73	87	3	60 65	33	02 46	1 28	22	17	79	47
13	58	14	70	5	53 64	6	20 20	23	60	26	03	33 2	40 50	30	32	41 73	70	1
15	45	22	75	2	60	13	80	12	72	19	76	22	50 60	17	34	15	76	2
16	49	21	63	ñ	50	24	00	12	12	17	,0	22	00	17	51	15	62	35
17	41	34	46	34	38	42	67	37	71	21	65	37			27	40	74	7
18	49	25	44	39	45	32	83	8	72	17	84	7	35	48	32	21	63	32
19	63	7	54	21	63	7	68	36	72	15	73	27	39	45	31	24	70	14
20	41	35	43	40	62	8	66	38	64	33	59	44	52	29	33	19	58	44
21	49	20	46	35	39	39	87	4	70	24	85	6	68	8	29	34	64	30
22	46	31	56	19	64	5	78	16	68	29	81	12	42	44	33	16	73	10
23	66	3	53	22	57	16	64	41	53	42	65	36	38	46	25	46	75	3
24	37	44	36	46	45	29	68	34	45	47	54	48	44	41	26	43	65	26
25	41	36	44	38	44	33	74	24	49	46	87	4	43	43	41	3	58	42
26	51	19	48	32	54	20	53	48	35	49	71	29	64	11	28	37	53	46
27	33	49	46	37	8	49	73	26	77	9	78	16	58	21	36	9	38	49
28	49	22	65	9	29	47	74	22	72	18	67	31	51	32	29	33	50	48
29	40	40	58	16	60	12	73	25	75	12	59	46	46	39	34	12	66	21
30	49	24	37	45	46	28	63	42	63 50	34	01	18	55	25	33	18	63 57	34 15
31	48	20	/3	3	29	40	59 79	44	5U 92	45	81 92	10	55	27	30	11	57	45
32	34	48	40	42	44 50	34	/8	15	83	2 42	83 70	10	50	24	28	30	60 60	30 15
23 24	03 40	20	32	23 19	24	14	39	45	55 71	43	/9 02	15	51	33	29	25	66	24
34	40 50	13	55	40 20	54 44	35	92 52	1	59	40	50 50	43	36	42	25	15	60	24 40
36	35	46	63	12	29	48	52 70	33	45	48	80	13	64	10	31	28	63	33
37	37	43	43	41	41	37	78	17	75	11	73	25	74	2	38	6	58	43
38	66	4	59	15	45	31	71	29	72	16	71	28	62	15	43	1	73	9
39	68	2	68	8	62	9	87	3	84	4	90	3	63	12	38	4	72	11
40	64	6	68	7	59	15	85	5	74	13	66	32	71	6	26	44	63	31
41	40	38	46	36	49	25	77	19	71	20	78	17	47	37	38	5	65	27
42	46	28	61	14	47	27	72	27	69	27	53	49	60	18	28	38	65	25
43	46	32	34	49	48	26	65	40	58	41	75	23	52	30	31	27	60	37
44	35	45	53	23	39	40	58	45	52	44	65	35	69	7	35	10	68	16
45	38	42	50	28	41	38	79	14	90	2	62	39	54	26	41	2	67	19
46	70	1	71	4	66	3	57	46	77	8	73	26	73	3	30	29	70	13
47	41	37	56	18	43	36	77	20	60	39	60	42	46	40	36	8	64	29
48	64	5	. 50	29	55	19	66	39	65	31	59	45	35	49	27	39	67	18
49	47	27	56	17	36	43	68	35	62 70	35	()	19	57	23	32	22	61	30
50							85	0	/ð	/	62	41	52	20	23	4/		
51													55 64	20 0				
														,				
Mean	50		53		49		73		68		73		55		31		65	

Table 4. Mean percentage survival (SURV, %) for each E. regnans provenance at each site together win	th rankings
(R). Local provenance at each site marked by bold.	0

Prov STR R S	Duran	BRO	WN	LIN	١K	TO	DL	GEE	EVE	NAT	ON	WOO	DLN	DEL	.OR	LOI	NE
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Prov	STR	R	STR	R	STR	R	STR	R	STR	R	STR	R	STR	R	STR	R
2 3.55 27 297 46 3.27 26 3.04 12 296 30 3.07 28 3.48 5 3 3.82 14 4.09 7 4.17 3 4.15 2 3.59 3 3.60 4 3.50 2 3.30 13 16 3.55 17 3.68 17 3 3.16 13 16 3.50 2 3.14 24 3.21 12 2.97 31 3.14 23 3.14 23 3.14 23 3.14 23 3.14 27 2.72 4.37 3 3.18 16 3.00 2.72 2.72 4.3 9 4.10 6 3.89 14 3.98 4 3.24 21 3.61 15 3.07 18 3.28 15 2.98 35 3.13 16 3.00 2.72 4.3 3.22 22 3.31 16 3.00 2.89 3.04 3.3 16 3.04 3.3 16 3.04 3.3 17 <	1	3.65	22	3.67	23	3.69	10	2.97	38	2.90	43	3.17	14	2.85	34	2.70	44
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	2	3.55	27	2.97	46	3.27	26	3.20	28	3.55	20	2.96	30	3.07	28	3.48	5
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	3	3.82	16	3.98	10	3.73	9	3.22	24	3.64	12	3.50	2	3.95	1	3.06	31
5 4.12 4 3.76 16 3.85 7 2.97 39 3.45 24 3.21 12 2.97 3.38 3.47 3 3.18 23 3.14 27 7 3.98 11 3.72 21 3.55 17 3.48 5 3.74 8 2.92 33 3.14 23 3.14 27 2.72 43 9 4.10 6 3.89 14 3.98 3.22 3.31 16 3.09 27 2.72 43 11 3.53 3.3 17 3.69 4 3.29 3.33 2.69 44 3.29 2.33 3.53 3.5 3.4 3.26 14 3.29 3.31 12 3.44 4 3.22 12 3.11 12 3.46 4 3.22 12 3.11 12 3.66 13.27 12.89 3.22 2.89 3.22 2.29 3.70 11	4	4.09	7	4.17	3	4.15	2	3.59	3	3.90	4	3.52	1	3.56	5	3.20	23
	5	4.12	4	3.76	16	3.85	7	2.97	39	3.45	24	3.21	12	2.97	31	3.25	18
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	6	4.09	8	4.51	1	3.68	12	3.39	10	3.38	28	3.47	3	3.18	23	3.14	27
8 4,17 3 4,06 6 3,62 14 2,99 35 3,63 13 3,13 16 300 27 2,72 43 10 3,51 31 4,01 8 3,45 22 3,59 4 3,79 6 3,22 9 2,83 35 3,24 13 11 3,53 30 3,75 17 3,69 11 3,26 19 3,29 31 2,69 44 4 3,32 12 3,11 16 3,04 33 12 3,43 6 3,94 11 3,94 6 3,47 6 4,06 2 3,44 4 3,32 12 3,11 28 41 13 46 2,44 4 3,32 12 3,11 18 3,26 28 11 3,35 21 3,02 25 3,00 16 3,34 7 2,89 33 2,89 31 2,84 41 2,13 3,55 2,84 14 3,13 37 18 3,12 </td <td>7</td> <td>3.98</td> <td>11</td> <td>3.72</td> <td>21</td> <td>3.55</td> <td>17</td> <td>3.48</td> <td>5</td> <td>3.74</td> <td>8</td> <td>2.92</td> <td>33</td> <td>3.14</td> <td>24</td> <td>3.75</td> <td>2</td>	7	3.98	11	3.72	21	3.55	17	3.48	5	3.74	8	2.92	33	3.14	24	3.75	2
9 4 1.0 6 3.89 14 3.98 4 3.24 21 3.61 15 3.07 18 3.28 15 2.98 35 10 3.51 31 4.01 8 3.45 22 3.59 31 2.69 44 3.29 13 3.04 33 12 3.43 36 3.39 37 3.27 27 3.05 32 3.74 9 3.04 43 3.22 12 3.11 28 13 4.12 2 4.18 2 4.32 1 3.31 15 3.70 11 3.36 6 2.79 38 2.86 41 15 3.06 9 3.29 3.11 28 3.02 25 3.00 28 3.22 21 3.02 25 3.08 29 3.17 25 3.69 3.22 21 3.29 3.17 25 18 3.20 3.21 23 3.52 29 3.00 28 3.22 21 2.23 3.52	8	4.17	3	4.06	6	3.62	14	2.99	35	3.63	13	3.13	16	3.09	27	2.72	43
	9	4.10	6	3.89	14	3.98	4	3.24	21	3.61	15	3.07	18	3.28	15	2.98	35
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	10	3.51	31	4.01	8	3.45	22	3.59	4	3.79	6	3.32	9	2.83	35	3.24	19
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	11	3.53	30	3.75	17	3.69	11	3.26	19	3.29	31	2.69	44	3.29	13	3.04	33
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	12	3.43	36	3.39	37	3.27	27	3.05	32	3.74	9	3.04	23	3.62	4	3.22	22
14 4.22 2 4.18 2 4.32 1 3.31 15 3.70 11 3.36 6 2.79 38 2.86 41 15 4.06 9 4.07 5 3.96 5 3.41 9 3.58 17 3.34 8 3.04 29 3.17 25 16 4.04 10 3.74 18 3.26 28 3.71 0 3.08 29 3.02 25 5 3.08 29 3.04 29 3.289 40 19 3.77 17 3.89 15 3.42 23 3.23 22 3.35 29 3.00 28 3.22 21 2.92 37 20 3.19 45 3.44 36 2.85 41 3.01 34 3.33 27.78 38 2.80 36 3.32 15 22 4.22 1 3.91 13 3.22 3.66 47 2.38 3.44 3.44 3.44 3.44 3.44 3.44	13	4.12	5	3.94	11	3.94	6	3.47	6	4.06	2	3.44	4	3.32	12	3.11	28
15 4.06 9 4.07 5 3.96 5 3.41 9 3.58 17 3.34 8 3.04 29 3.17 25 16 4.04 10 3.73 19 3.08 25 28 3.02 25 3.08 29 3.08 29 3.7 3.60 16 3.34 8 3.04 29 3.289 3.02 25 3.08 2.89 33 2.89 33 2.89 33 2.89 33 2.89 33 2.89 33 2.89 33 3.49 7 3.32 14 21 3.55 8 3.44 2.88 39 3.22 23 3.63 14 2.69 43 3.49 7 3.32 14 21 3.55 29 3.49 13 3.60 25 3.67 2 3.38 27 2.71 14 3.25 17 3.26 17 3.22 2.93 2.25 47 2.66 47 2.87 36 2.34 49 2.88	14	4.22	2	4.18	2	4.32	1	3.31	15	3.70	11	3.36	6	2.79	38	2.86	41
16 4.04 10 3.74 18 3.26 28 17 3.76 18 3.88 26 3.99 3 2.93 41 3.53 21 3.02 25 3.08 29 18 3.96 13 3.73 19 3.08 35 2.98 37 3.60 16 3.34 7 2.89 33 2.89 40 19 3.77 17 3.89 15 3.42 23 3.23 22 3.35 29 3.00 28 3.22 21 2.92 3.1 1.4 21 3.55 28 3.42 36 2.85 41 3.01 34 3.13 37 2.78 38 2.80 36 3.327 17 24 3.43 35 3.52 29 3.49 19 3.21 26 3.57 18 3.01 27 2.75 39 2.28 44 9 2.89 39 27 3.21 43 3.10 45 2.29 48	15	4.06	9	4.07	5	3.96	5	3.41	9	3.58	17	3.34	8	3.04	29	3.17	25
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	16	4.04	10	3.74	18	3.26	28										
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	17	3.76	18	3.58	26	3.99	3	2.93	41	3.53	21	3.02	25			3.08	29
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	18	3.96	13	3.73	19	3.08	35	2.98	37	3.60	16	3.34	7	2.89	33	2.89	40
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	19	3.77	17	3.89	15	3.42	23	3.23	22	3.35	29	3.00	28	3.22	21	2.92	37
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	20	3.19	45	3.45	34	2.88	39	3.22	23	3.63	14	2.69	43	3.49	7	3.32	14
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	21	3.55	28	3.42	36	2.85	41	3.01	34	3.13	57	2.78	38	2.80	36	3.32	15
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	22	4.22	1	3.91	13	3.20	30	3.42	8	4.16	1	3.06	20	3.88	3	3.47	6
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	23	3.98	12	3.50	31	3.36	25	3.67	2	3.38	27	2.71	41	3.25	1/	3.26	17
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	24	3.43	30	3.52	29	3.49	19	3.21	26	3.37	18	3.01	27	2.75	39	2.58	4/
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	25	3.80	14	3.71	40	3.10	33	3.21	27	3.72	10	2.93	32	2.58	44	3.44	9
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	20	2.57	49	2.73	49	2.43	40	2.73	47	2.00	4/	2.87	30	2.34	49	2.89	39
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	27	3.21	43	3.10	45	2.29	48	2.93	40	3.24	32	2.55	4/	3.22	20	3.28	10
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	20	2.70	47	J.19 4 10	45	2.23	49	2.95	42 20	2.21	49	2.45	49	3.41	42	3.45	12
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	29	2 14	21	3 28	30	3.02	13	3.14 2.96	29 45	2.90	42	2.94	31 45	2.09	45	2.30	12
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	30	3.44	38	2.20	18	2.05	44	2.80	45	2.80	36	3.02	21	2.45	ν η / Ω	2.05	12
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	32	3.44	33	3 46	33	2.05	31	3 35	11	3.52	20	2 79	37	2 90	32	2.55	36
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	32	3.86	15	3.50	30	3.17	37	3.33	16	3.18	35	2.77	30	3 45	0	3 14	11
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	34	3.00	42	3 18	44	2.61	45	3.20	25	3 44	25	2.77	40	3.93	2	3.57	3
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	35	3 33	41	3 20	42	2.01	36	3.26	18	3.06	39	2.74	42	3 29	14	3 44	8
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	36	3.58	25	4 01	7	3.66	13	2.85	46	3.95	3	3.06	22	3.12	26	3 22	20
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	37	3 46	32	3 24	40	2.65	43	3 27	17	2.67	46	2.60	46	3 22	19	3 50	4
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	38	3.71	20	3.55	28	2.92	37	3.34	13	3.10	38	3.17	15	2.79	37	3.44	10
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	39	3.72	19	3.94	12	3.85	8	3.44	7	3.56	19	3.06	21	3.55	6	3.22	21
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	40	3.64	23	3.99	9	3.46	21	3.35	12	3.40	26	3.38	5	3.13	25	3.03	34
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	41	2.64	48	2.89	47	2.37	47	2.72	48	2.44	48	2.87	35	2.46	48	2.82	42
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	42	3.36	40	3.73	20	3.49	20	2.92	43	3.20	34	3.11	17	2.73	41	2.91	38
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	43	3.57	26	3.20	41	3.09	34	2.98	36	3.21	33	3.07	19	2.72	42	3.04	32
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	44	3.42	37	3.49	32	3.52	18	3.11	30	3.35	30	3.20	13	2.75	40	2.57	49
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	45	3.39	39	3.42	35	2.90	38	3.09	31	2.99	41	2.90	34	3.25	16	2.58	48
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	46	3.53	29	3.64	24	3.60	16	3.32	14	3.74	7	3.02	26	3.37	11	3.15	26
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	47	3.12	46	3.38	38	3.21	29	2.71	49	2.78	45	3.29	10	2.98	30	3.19	24
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	48	3.60	24	3.56	27	3.40	24	3.24	20	3.46	23	2.99	29	3.38	10	2.65	45
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	49	3.20	44	3.62	25	2.69	42	3.04	33	3.02	40	2.51	48	3.22	18	3.08	30
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	50							3.95	1	3.84	5	3.23	11			4.14	1
52 2.54 46 Mean 3.61 3.61 3.30 3.18 3.37 3.01 3.09 3.14 s.d. 0.35 0.26 0.36 0.28 0.37 0.32 0.33 0.32	51													2.58	45		
Mean 3.61 3.30 3.18 3.37 3.01 3.09 3.14 s.d. 0.35 0.26 0.36 0.28 0.37 0.32 0.33 0.32	52				_									2.54	46		
s.d. 0.35 0.26 0.36 0.28 0.37 0.32 0.33 0.32	Mean	3 61		3.61	-	3 30		3 18		3 37		3.01		3 00		3.14	
	s.d.	0.35		0.26		0.36		0.28		0.37		0.32		0.33		0.32	

 Table 5. Mean stem straightness score (STR) for each E. regnans provenance at each site together with rankings (R).

 Local provenance at each site given in bold.

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Dear	BRO	WN	LIN	١K	TO)L	GEE	VE	NAT	ON	WOO	DLN	DEL	OR	LOI	NE
Prov	BRN	R	BRN	R	BRN	R	BRN	R	BRN	R	BRN	R	BRN	R	BRN	R
1	3.49	41	3.52	33	3.61	37	3.01	31	2.68	46	3.25	13	3.28	25	2.94	37
2	3.55	38	3.84	17	3.62	35	3.16	17	3.19	20	3.69	1	3.66	5	3.34	10
3	3.83	22	3.79	20	3.72	30	3.20	15	2.83	44	3.15	26	3.77	3	3.05	30
4	4.13	9	3.94	10	4.24	5	2.92	37	2.92	39	3.01	35	3.32	21	3.10	26
5	3.96	16	3.85	14	3.56	38	2.81	41	3.07	32	2.99	37	3.18	36	3.16	23
6	3.67	36	4.18	2	4.30	2	3.06	25	3.00	34	2.92	40	3.40	16	2.95	36
7	3.80	26	3.46	36	3.76	28	3.32	7	3.60	6	3.27	11	3.51	12	3.63	5
8	4.35	2	3.86	13	3.81	26	3.28	11	3.09	30	2.85	42	3.33	20	2.70	45
9	3.99	14	4.06	8	3.86	23	2.62	47	3.00	33	2.83	43	3.09	43	2.84	39
10	4.25	3	3.87	11	4.27	4	3.30	9	3.59	7	3.24	15	3.84	1	2.80	42
11	4.23	4	4.02	9	3.82	25	2.92	36	2.84	42	3.17	22	3.25	28	2.72	43
12	3.81	25	3.59	32	3.34	46	3.06	27	3.66	2	3.24	16	3.53	11	3.22	18
13	3.81	24	3.75	24	3.93	21	3.15	18	3.23	17	3.28	10	3.17	39	3.03	32
14	4.14	7	4.08	7	4.03	14	2.99	33	3.60	5	3.08	31	3.22	30	2.63	48
15	4.00	13	3.76	23	4.35	1	3.10	21	3.13	24	2.92	39	3.20	32	2.89	38
16	4.03	11	3.85	15	3.98	18										
17	4.46	1	3.66	28	4.18	6	2.85	40	3.00	35	2.79	45			2.67	47
18	4.02	12	4.18	4	3.97	20	2.67	45	3.32	9	3.38	6	3.31	22	2.58	49
19	3.71	34	3.48	34	3.97	19	2.94	34	2.84	43	3.31	8	3.25	27	2.81	41
20	3.79	30	3.82	19	3.77	27	3.27	13	3.64	3	3.16	23	3.29	24	3.52	8
21	3.38	45	2.89	49	3.71	32	3.43	5	3.11	28	2.70	47	3.15	40	3.04	31
22	3.79	28	3.45	37	3.06	48	3.49	3	3.26	13	3.38	5	3.46	13	3.26	14
23	3.43	44	3.31	43	3.69	33	2.68	44	3.73	1	3.24	17	3.27	26	3.50	9
24	2.85	49	3.69	26	3.41	43	3.27	12	3.13	26	3.13	29	3.23	29	3.01	34
25	3.50	40	3.48	35	3.34	45	2.89	39	2.88	40	3.06	32	3.12	42	3.28	13
26	3.94	18	3.45	39	4.15	8	2.37	49	2.37	49	3.23	19	2.34	49	2.69	46
27	3.19	48	3.64	31	3.37	44	2.74	43	3.25	14	3.20	20	3.66	4	3.10	25
28	4.13	8	3.31	44	3.71	31	3.04	29	2.55	48	3.04	33	3.55	10	3.73	3
29	4.08	10	3.77	21	4.07	13	3.28	10	2.94	37	3.09	30	3.17	37	3.08	28
30	3.95	17	4.18	3	3.75	29	3.01	32	3.07	31	2.71	46	3.14	41	2.81	40
31	3.83	23	2.99	48	3.53	40	2.62	46	3.22	19	2.87	41	3.19	34	3.57	7
32	3.47	42	3.45	38	3.51	41	3.06	26	3.15	21	3.16	24	3.39	18	3.19	21
33	3.79	29	3.66	27	3.98	17	3.15	19	3.39	8	3.13	28	3.04	44	3.23	17
34	3.20	47	3.28	45	2.92	49	3.45	4	3.24	15	3.15	25	3.79	2	3.99	1
35	3.71	33	3.31	42	3.43	42	3.05	28	3.09	29	3.43	4	3.45	15	3.24	15
36	3.45	43	4.08	6	3.85	24	2.81	42	2.78	45	2.47	49	3.37	19	3.01	35
37	3.86	20	3.19	47	3.55	39	3.31	8	3.27	12	3.01	36	3.57	8	3.87	2
38	3.98	15	3.85	16	3.62	36	3.13	20	3.30	11	3.33	7	3.59	6	3.61	6
39	3.53	39	3.64	30	4.10	12	3.23	14	3.32	10	2.92	38	3.39	17	3.24	16
40	3.74	32	3.65	29	3.99	16	3.01	30	3.23	18	3.25	14	3.19	33	3.01	33
41	3.21	46	3.82	18	3.28	47	3.18	16	3.15	22	3.02	34	3.18	35	3.22	19
42	3.85	21	4.15	5	4.30	3	3.35	6	2.87	41	3.65	2	3.03	45	3.32	11
43	4.23	5	4.41	1	4.03	15	3.70	2	3.24	16	3.30	9	2.98	47	3.19	22
44	3.63	37	3.25	46	4.17	7	2.93	35	3.13	25	3.26	12	2.99	46	2.71	44
45	3.70	35	3.73	25	4.12	10	3.07	23	3.15	23	3.23	18	3.59	7	3.08	27
46	3.77	31	3.87	12	4.13	9	3.09	22	3.63	4	3.55	3	3.17	38	3.21	20
47	3.79	27	3.36	40	4.11	11	2.56	48	3.11	27	3.14	27	3.46	14	3.11	24
48	3.87	19	3.34	41	3.91	22	2.91	38	2.93	38	3.20	21	3.56	9	3.29	12
49	4.21	6	3.76	22	3.65	34	3.06	24	2.98	36	2.56	48	3.29	23	3.06	29
50							3.82	1	2.67	4 /	2.80	44	2.50	40	3.67	4
51													2.39	48		
													3.20	51		
Mean	3.80		3.68		3.81		3.07		3.13		3.12		3.30		3.14	
s.e	0.32		0.32		0.30		0.26		0.36		0.31		0.32		0.28	
	0.00				0.00	_	0.20		0.00		U.D I		0.04		0.20	

Table 6. Mean branch quality score (BRN) for each E.	regnans provenance at each site together with rankings (R).
Local provenance given in bold.	

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enclosed in a box.

At each site the local provenance was generally not amongst the best- performing provenances for diameter. The exception was at Womerah Rd, where the local provenance ranked top for DBH. At Browntown, Linkletters, Toolangi and Lone Star the local provenance appeared in the top ten rankings for DBH. However, at the remaining sites the local provenances performed poorly.

Across all sites the Strzelecki Ranges provenances (22, 23 and 50) generally performed well for DBH (Table 3). Mirboo East (22) ranked in the top ten for DBH at Browntown, Toolangi, Geeveston, Natone, Woolnorth, Deloraine and Lone Star. Traralgon Creek (23) also ranked in the top 10 for DBH at Browntown, Linkletters, Toolangi, Geeveston, and Womerah Rd. For Gunyah (50), rankings were also relatively high being ranked first at Woolnorth and fifth at Natone.

For the Tasmanian sites two additional provenances performed well for DBH. Both Mt Erica 490 m (12) and Toolangi (3) were well above the site means. In addition, two groups of Tasmanian provenances ranked well at a subset of sites. The first group from north –east Tasmania contains Ben Nevis (33), Forester (34) and Dans Valley (35), which ranked highly at Geeveston, Woolnorth, Deloraine and Lone Star. The second group from south-west Tasmania contained the Florentine Valley (38), Styx (39) and Moogara (40) which again ranked well at some sites.

The poorest provenances for DBH were Mt Useful (11), Quarry Creek (15), Buchan (17), New Haven (27), Stoneyhurst Creek (42) and Otway Messmate (26) with the exception of Lone Star. Buchan (17) was notable for being consistently among the lowest 15 ranks out of 49 at all 8 sites where it was planted. At the Tasmanian sites Mt Toorongo Track (9) and Fern Tree (44) also performed poorly.

Mean survival (Table 4) was generally low across all sites, ranging from a maximum of 73% at both Geeveston and Woolnorth to only 31% at Lone Star. Local provenances were again not amongst the best except at Womerah Rd. Overall, provenances that showed highest survival at all sites were Styx (39), Valencia Creek (14) and Levendale (46).

For stem straightness (Table 5) the Narbethong (4) provenance appeared outstanding, ranking in the top 7 at 7 out of the 8 sites assessed, with Lone Star being the exception. Other provenances that performed well were Valencia Creek (14) which ranked first or second at the Victorian sites but poorly in Tasmania and Mt Erica 990 m (13 and 16) which ranked well at most sites. The four provenances which were consistently among the worst for stem straightness were Otway Messmate (26), Christmas Hills (30) and Strathblane (41) which

performed badly at all sites and Ferndene (28) which was poor at all sites except Lone Star and Deloraine.

Results for branch quality (Table 6) indicated no pattern across the sites and no provenance appeared outstanding for this trait. Rankings of provenances changed dramatically between sites making any general conclusions difficult. An example is the branch quality rankings for Forester (34) which changed from first and second at Lone Star and Deloraine to 49 at Toolangi.

Correlations between sites

Correlations between provenance means for DBH, survival, stem straightness and branch quality scores across sites are presented in Table 7. For stem straightness there were significant positive correlations between all sites with the exception of the poorest site (Lone Star). However, for both branch quality and DBH the correlations were generally low and nonsignificant.

Genotype by environment analyses

Analyses of variance

Results for analyses of variance across sites are presented in Table 8. Provenance, site and the provenance by planting site interaction were significant for both diameter and survival. When provenances were grouped by state of origin (Victoria or Tasmania) there were no significant differences between the states but significant provenance within state effects for both diameter and survival; indicating no systematic difference between these two groups.

Joint regression analyses

For diameter the results (Figure 2) indicate some clustering of provenances is possible but to a limited extent. The closest grouping is the two Otway populations (24 and 25) which had relatively high regression coefficients indicating they are unstable but are only average in performance across all sites. The other apparent grouping is the outlying populations in eastern Victoria (10, 11, 14, 15, 17, 18, and 19) which all produced low means and regression coefficients between 0.9 and 1 indicating that these populations were relatively stable but poorly adapted to all environments. For the remaining provenances, it was not possible to form any other geographic groupings from the results in Figure 2. Tasmanian and Victorian provenances were intermixed across the range of mean and regression coefficients with no clear boundaries.

The best performing provenances (highest means)

C. A. F	AYMOND ET AL.	PROVENANCE	VARIATION AND	$G \times F$	E INTERACTIONS IN	EUCALYPTUS REGNANS
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				S	ITE			
	BROWN	LINK	TOOL	GEEVE	NATONE	WOOL	DELOR	LONE
DBH								
LINK	0.38**							
TOOL	0.48**	0.33*						
GEEVE	0.01	0.31	0.24					
NATONE	0.019	0.40**	0.66**	0.48**				
WOOL	0.59**	0.53**	0.51**	0.24	0.50**			
DELOR	0.11	0.14	0.39**	0.47**	0.54**	0.39**		
LONE	0.21	0.28	0.24	0.53**	0.33*	0.49**	0.28	
WOMER	0.45**	0.58**	0.42**	0.29*	0.46**	0.57**	0.20	0.23*
SURVIVAL								
LINK	0.38**							
TOOL	0.49**	0.13						
GEEVE	-0.16	-0.04	0.03					
NATONE	0.13	0.06	0.04	0.12				
WOOL	-0.04	-0.19	-0.07	0.39**	0.18			
DELOR	-0.03	0.14	0.05	0.13	0.10	0.09		
LONE	-0.21	-0.10	-0.12	0.13	0.11	0.31*	0.08	
WOMER	0.45**	0.35*	0.57*	0.05	0.14	-0.04	-0.16	-0.03
STR								
LINK	0.75*							
TOOL	0.75**	0.79**						
GEEVE	0.59**	0.52**	0.49**					
NATONE	0.69**	0.58**	0.64**	0.57**				
WOOL	0.55**	0.61**	0.71**	0.24	0.50**			
DELOR	0.25	0.17	0.14	0.40**	0.41**	0.02		
LONE	0.08	-0.08		0.29*	0.11	-0.22	0.37**	
BRN								
LINK	0.37*							
TOOL	0.47**	0.38*						
GEEVE	-0.02	0.10	-0.15					
NATONE	-0.07	0.02	-0.09	0.27				
WOOL	-0.06	0.02	0.03	0.14	0.24			
DELOR	0.11	0.11	-0.32*	0.29*	0.29*	0.09		
LONE	-0.25	-0.43**	-0.48*	0.31*	0.23	0.14	0.40**	

Table 7. Correlations between provenance mens at each site for diameter (DBH), survival, stem straighntess (STR), and branch quality (BRN).

in Figure 2 were Mirboo East (22), Forester (34) and Goulds (37). Of these Mirboo East had a regression coefficient very close to 1 indicating that this provenance is well adapted to all environments and stable. The other two are more unstable, having regression coefficients around 1.1.

Grouping of provenances

Grouping provenances using Chappill's system based on morphological differences also resulted in no significant differences between the groups for diameter. For survival, Chappill's grouping gave a significant group effect but a non-significant provenance within group effect.

The geographic grouping, based on an extension of WILCOX (1982) groups, however, did result in a significant group effect for both diameter and survival. However, there was also a significant group by site interaction. When sites were analysed separately, the group effects were significant at only four sites for DBH and two sites for survival. Examination of the group means for each site indicated little difference between 6 out of the 7 groups for DBH at each site. For

Table 8. Analyses of variance across sites for diameter at breast height (DBH) and percentage survival (SURV) for *Eucalytpus regnas*

Source	DI	ЗН	Sur	vival
Source	DF	MS	DF	MS
ALL PROVENANCES & ALL S	ITES			
Site	8	1098.64**	8	8667.94**
Provenance	46	8.73**	46	193.80**
Site by Provenance interaction	367	1.36**	367	92.35**
Pooled Residual		0.87		38.13
PROVENANCES GROUPED BY	STATE OF O	RIGIN		
Site	8	1098.64**	8	8667.94**
State	1	1.60	1	340.82
Provenance within State	45	8.89**	45	190.54**
Site by Provenance interaction	367	1.36**	367	92.35**
Pooled Residual		0.87		38.13
CHAPPILL'S GROUPINGS				
Site	8	636.09**	8	4812.5**
Group	4	17.49	4	508.5**
Provenance within Group	17	9.98**	17	117.5
Residual	168	1.66	168	103.4
GEOGRAPHIC GROUPINGS				
Site	8	1098.64**	8	8667.94**
Group	6	25.22**	6	538.28**
Provenance within Group	40	6.26**	40	142.13**
Site by Group interaction	48	2.16**	48	144.48**
Site by Provenance interaction	319	1.19**	319	84.51**
Pooled Residual		0.87		38.13



Figure 2. Joint regression analysis for diameter at 1.3 m for *E.regnans* provenances planted at nine sites in south-eastern Australia.

the sites where the group effect was significant, a different group appeared responsible at each site.

Correlations with earlier data

Correlations are presented in Table 9. For FROST and SURV correlations ranged from -0.15 to 0.57 and were significant for those sites which were above 400 m in altitude – Browntown Rd, Linkletters Rd, Toolangi and Womerah Rd. However, at the lower altitude sites the correlations were non-significant. For HT-1 and DBH, the correlations were significant at all sites with the exception of Womerah Rd. However, whilst the correlations were significant their size was generally low to moderate, ranging from 0.308 for Browntown Rd to 0.607 for Natone.

Table. 9 Correlation between percentage survival (SURV) at ages 9 to 13 years and frost damage assessed at age one year (FROST-1) and height growth at age one year (HT-1) and diameter at 1.3 m (DBH) at ages 9 to 13 years for *E. regnans*

SURV and FROST-1	DBH and HT-1
0.44**	0.31*
0.52**	0.41**
0.39**	0.52**
0.04	0.51**
0.28	0.61**
-0.15	0.54**
0.09	0.46**
-0.13	0.32*
0.57**	0.27
	SURV and FROST-1 0.44** 0.52** 0.39** 0.04 0.28 -0.15 0.09 -0.13 0.57**

DISCUSSION

The two-stage breeding strategy proposed by GRIFFIN (1983a) appears to have been based on several assumptions: (i) that large provenance differences were expected, (ii) that these differences would form patterns within the natural range of the species and (iii) it would be possible for provenances to be grouped into geographic areas.

The results presented here do not support these assumptions as no systematic patterns or geographic grouping of provenances appears possible even though provenance differences have been demonstrated. Significant interactions were found between provenances and sites. However, no group of provenances was best at all sites for any of the traits assessed. Attempts to group provenances by geographic regions was generally not successful and could not explain the observed interactions of provenances and sites. Each site produced a different set of rankings resulting in generally low and non-significant correlations between sites for DBH and branch quality. A similar lack of pattern of provenance performance across sites in E. regnans was reported by PEDERICK (1988, 1990) in studies of families from Victoria grown at Toolangi and assessed at ages 8 and 10. The growth of most families was very good but the observed variation in growth between provenances could not be associated with site factors.

In contrast, stem straightness appeared to be less affected by site with correlations between most sites being significant. These results indicate that tree characteristics may be affected differentially by environmental factors. For example, growth and fitness traits should be positively related to adaptation, but quality traits such as stem straightness and branch retention are probably neutral to adaptation (PEDERICK 1990).

Local provenances did not perform well at most sites in this study, with the exception of Womerah Rd. A similar result was found by PEDERICK (1988) in trials of Victorian provenances. The failure of local provenances is not unexpected given that local populations have undergone natural selection to maximise reproductive fitness, which may or may not be correlated with vigour (NAMKOONG 1969).

Original seed collection records were available for 41 of the provenances reported here. These records indicated that Buchan (17), Carisbrook (24), Upper Ford River (25), Lorinna (29), Ben Nevis (33), Dans Valley (35), Royal George (36) and Murdunna (49) were all collected from previously logged stands suggesting that the remaining trees may have been rejected for logging due to poor quality. Following such logging the level of outcrossing may have been significantly reduced (as few trees remain) leading to depressed growth due to inbreeding. Of the above provenances Buchan, Carisbrook, Upper Ford River, Royal George and Murdunna had all been relatively recently logged and all performed relatively poorly in the trials reported here. In contrast Dans Valley and Ben Nevis, which had been logged many years before, performed amongst the best provenances. However, the provenances showing poor performance also come from outlying populations of E. regnans.

The sampling strategy adopted across the restricted and discontinuous distribution of *E. regnans* was to intensively sample the isolated outlier populations (GRIFFIN *et al.* 1982). The hypothesis was that within such populations random genetic drift or hybridisation could become important determinants of the populations characteristics. It is thus important to examine the performance of outlier populations relative to larger centres of distribution.

One of the worst-performing provenances, New Haven (27), is an outlier population being the most westerly of the Tasmanian collections. Behaviour of other outlier populations also tends to indicate that these populations generally do not perform amongst the best across all sites. For the outlier populations from eastern Victoria [Barkly River (10), Mt Useful (11), Valencia Creek (14), Quarry Creek (15), Buchan (17), Yalmy River(18) and Bendoc(19)] the performance of most, with the exception of Bendoc (19), was generally poor, being in the bottom 50% of provenances ranked for DBH. In addition, the Otway provenances [Carisbrook (24), Upper Ford River (25) and Otway Messmate (26)] generally ranked poorly across all sites. However, for the outlier populations in central Victoria [Mt Disappointment (1), Kallista (2) and Wilson's Promontory (21)] performance across sites was highly variable with good DBH some sites and poor DBH on other sites.

For the outlying provenances in Tasmania [New Haven (27), Ferndene (28), Lorinna (29), Christmas Hills (30), Beaconsfield (31), Royal George(36), Stoneyhurst Creek (42), Bruny Island (45) and Murdunna (49)] performance was again generally poor, particularly for New Haven, Royal George and Murdunna which ranked in the bottom 50% at most sites for DBH.

In contrast, the best-performing provenances originated from larger continuous areas of the distribution. In Victoria good performance was shown by provenances from the Strzelecki ranges area [Narracan (20), Mirboo East (22), Traralgon Creek (23) and Gunyah (50)] plus Mt Erica (12 and 13). In Tasmania the best provenances originated from the north-east [Ben Nevis (33), Forester (34), Dans Valley (35) and Goulds Country (37)] and the south-west [Florentine Valley (38), Styx (39) and Moogara (40)].

Unfortunately the seed collection records were not available for the poorly-performing New Haven (27) provenance. However, only three trees were included in the original seed collection. For the provenances which were both from outlying populations and heavily logged (Buchan, Carisbrook, Upper Ford River, Royal George and Murdunna) the poor performance shown in these trials may be due to either of these factors or a combination of both. For these populations it is not possible to separate the effects of the logging from the effects of being an outlier. However, the results presented here suggest that collection of seed from such sites is not a good strategy as potentially increased levels of inbreeding in these populations may result in lower performance. The potential contribution these populations could make to a breeding program is not evident in the first generation and may only become evident after wide outcrossing leading to a subsequent release from inbreeding.

The two-stage strategy developed by GRIFFIN (1983a) appears to be unnecessary for this species. A better option would be to combine Stages One and Two and to establish combined provenance/progeny trials where families from many different provenances were established in a large trial as the initial population in a breeding program. Such an approach is currently recommended for use in eucalypt breeding programs (RAYMOND 1988, 1991) and has been successfully used by FRANKLIN and MESKIMEN (1983) for *E. grandis* in Florida. This option has the advantage of allowing outcrossing between trees from widely separated populations, provided flowering times overlap. By combining both stages there is no time lag in starting

the actual selection and mainstream breeding activities that lead to the production of improved seed. In the two-stage strategy presented by GRIFFIN (1983a), a time lag of between five and ten years is required between the establishment of the initial provenance trials and the establishment of the breeding population for the first generation of the breeding program. This time lag is due to having to wait until the provenance trials are sufficiently old to allow reliable assessment of provenance performance and genotype by environment interactions. Once superior provenances are identified there is the need to go back to these areas and undertake extensive single-tree seed collections to form the breeding population.

In contrast to the studies of frost tolerance in E. regnans which found a trend for increasing tolerance to frost with increasing altitude of provenance origin (ELDRIDGE 1968, 1972 and GRIFFIN et al. 1982), no systematic patterns in provenance performance are evident in this study. This lack of patterns and the existence of genotype by environment interactions makes it extremely difficult to recommend provenances for use across a range of sites. This may indicate either that E. regnans is extremely site specific or alternatively that there are no major differences between the provenances which are strongly related to environmental characteristics. As the natural range of *E. regnans* is severely restricted by climatic and soil factors the second option may be more likely and differences between provenances may not be related to their site of origin. Either option makes it extremely difficult to choose which provenance(s) should be used at a particular site.

Based on the results of this study it is not possible to develop rules for allocation of provenances to breeding zones or breeding populations for different sites. The best option would appear to be to exclude the poorer performing provenances and include most of the remaining provenances. If planting sites are high altitude the correlation between early frost damage score and subsequent survival must be accounted for by selecting only the more hardy provenances. However, if planting sites are lower in altitude, then all provenances found to be acceptable for growth rate should be included. However, if the eastern Victorian outliers are growing poorly due to increased levels of inbreeding their true merit should be evaluated by forcibly outcrossing these provenances.

The question remains of how best to constitute a breeding population for this species. Two options are available: firstly to assume that there will be good families within many provenances or secondly to select provenances which perform reasonably well across many sites and use these as the basis for the breeding population. The first option appears to be that which was followed for E. regnans in New Zealand (Cannon and SHELBOURNE 1991) where progeny trials of 300 open-pollinated families were established. Families included in the trials come from both second-generation selections and first-generation families from Australia and New Zealand. The second option has been followed for E. regnans in Australia. Based on growth at all sites at age 5 years (Griffin 1983b) and frost tolerance scored at one site at age 1 year (GRIFFIN et al. 1982) two provenance areas were selected to form the breeding population for use in Tasmania. Provenances selected were the Strzelecki Ranges provenances (22 and 23, Mirboo East and Traralgon Creek) which are fast growing but are somewhat frost tender and the Moogara provenance (40) from Tasmania with is above average for both growth and frost tolerance. New collections of seed from each of these regions have been undertaken and progeny trials established on a range of sites in Tasmania (HAND et al. 1989).

These selected provenances are still performing well in this current study at age 9-13 years. Based on both DBH and stem straightness, Mirboo East (22) is the best provenance across all sites (Figure 2). Moogara (40) also performs well for DBH but not as well as Mirboo East for stem straightness. The south Gippsland provenances were also found by PEDERICK (1988) to grow faster than other Victorian provenances in some (though not all) trials.

CONCLUSIONS

Provenance differences for DBH, stem straightness and branch quality were found at most sites for these *E. regnans* trials. However, provenance rankings differed from site to site and trait to trait and no single group of provenances was found to be best at all sites for any of the traits assessed. Several provenances (Buchan, New Haven and Otway Messmate) were consistently poor at all sites. Local provenances did not perform amongst the best at eight out of the nine sites. Outlying and recently logged populations tended to be among the poorer performers. Provenance differences do not appear to follow any systematic pattern and no geographic grouping of provenances is possible.

Based on DBH and stem straightness the bestperforming provenances were from Mirboo East and Gunyah in Victoria and Forester in Tasmania.

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