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Genetic control of coppice and lignotuber development in *Eucalyptus globulus*

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Abstract. The economics of short-rotation pulpwood plantations of *Eucalyptus globulus* as a coppice crop are influenced by stump survival and subsequent coppice growth rates. This study revealed significant genetic diversity in coppicing traits, both within and between subraces, following felling in a progeny trial after 9 years of growth. A total of 67% of trees coppiced after 14 months, but subraces varied from 43 to 73%. Heritabilities for coppice success (0.07) and subsequent growth (0.16–0.17) were low but statistically significant. Strong genetic correlation between presence/absence of coppice, the number of stems coppicing from the stump and modal coppice height, indicate that selection is possible by using the binary trait. The ability of a tree to coppice was genetically correlated with tree growth prior to felling ($r_g = 0.61$) and with nursery-grown seedling traits, where large genetic differences were observed in the development of lignotubers. Coppicing was genetically correlated with the number of nodes with lignotubers ($r_g = 0.66$) and seedling stem diameter at the cotyledonary node ($r_g = 0.91$). These traits were uncorrelated with later age growth and with each other. The results suggest that coppicing is influenced by three independent mechanisms—lignotuber development, enlargement of the seedling stem at the cotyledonary node and vigorous growth—which enhance ability to survive catastrophic damage, and indicate that both lignotuber and coppice development can be altered by both natural and artificial selection.

Introduction

When felled near the ground, many hardwood trees regenerate through coppice shoots that sprout from the stump (Blake 1983). Eucalypts are no exception (Hillis and Brown 1978), although the epicormic bud-producing structures appear unique to the genus (Burrows 2002). Eucalypt plantations are often managed for coppice production, be it to produce cut foliage in floriculture (Wirthensohn and Sedgley 1998), logs for fuelwood, or pulpwood (Doughty 2000). While most plantations of the major pulpwood species *Eucalyptus globulus* are managed by replanting following harvesting, there are references to *E. globulus* being managed as a coppice crop in India (Matthews 1992), Portugal (Turnbull and Pryor 1984; Almeida *et al.* 1990) and Chile (Turnbull and Pryor 1984; Prado *et al.* 1990; Alarcón 1994). In India, *E. globulus* has been coppiced four times on a 10–15-year cutting cycle (Doughty 2000), but pulp-production plantations tend to be coppiced only two or three times on rotations of 8–12 years, before replanting (Eldridge *et al.* 1993). Coppice regrowth derives considerable benefit from an established root system. Biomass production is initially greater than seedlings (Blake 1980; Crombie 1997) and yield from the first coppice crop often exceeds that from the maiden crop (Hillis and Brown 1978). However, yield on a per hectare basis is usually reduced, particularly in later rotations, owing to cumulative mortality of stumps rather than loss of vigour in living stumps (Matthews 1992).

Manipulation of coppicing requires knowledge of the genetic control and interrelationship amongst traits directly or indirectly affecting coppice production. One such trait, amenable to early selection, is lignotuber development. Lignotubers are woody swellings found in the axils of the cotyledons (Boland *et al.* 1984) on seedlings, which become buried as they develop, providing trees with a bank of meristematic tissue protected from lethal fire temperatures by an overlying mantle of soil (Noble 2001). These organs have long been believed to enhance regeneration by coppice and, along with bark, enhance survival of catastrophic events such as fire, drought, frost and browsing of seedlings in

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Table 1. Details of the subrace classification (modified from Dutkowski and Potts 1999) used in this study

The number of families per subrace in the Massy Greene trial (MG), the number of families for which data on coppice production was available (coppice), the number of families with lignotuber formation (lig) and the total number of families providing data used in the study (total)

Subrace location	Number of families			
	MG	Coppice	Lig	Total
Far Western Otways	6	5		6
Western Otways	120	92		120
Cape Patton	18	17		18
Eastern Otways	23	17	8	24
Strzelecki Ranges	58	43	8	58
Strzelecki Foothills	8	7		8
Gippsland Coastal Plain	13	10		13
Gippsland Foothills	3	3		3
Flinders Island	61	48		61
Southern Furneaux	50	39	1	50
St Helens	11	9	7	11
North-eastern Tasmania	19	15	15	25
Inland north-eastern Tasmania	20	17	7	20
Dromedary	4	3		4
South-eastern Tasmania	61	51		61
Southern Tasmania	27	19	20	32
Tasman Peninsula	5	3		5
Recherche Bay	4	3	6	9
Port Davey	6	2		6
Western Tasmania	29	27	7	29
King Island	32	29	8	32
Total	578	459	87	595

eucalypts (Kirkpatrick 1975; Jacobs 1979; Blake 1983; Noble 1984; Webley *et al.* 1986). Large genetically based differences in lignotuber development have been reported between (e.g. Burgess and Bell 1983; Noble 2001) and within (e.g. *E. viminalis*, Ladiges and Ashton 1974; *E. globulus*, Kirkpatrick 1975; *E. camaldulensis*, Jacobs 1979; and *E. gunnii*, Potts 1985) eucalypt species. Intraspecific variation in coppice production has also been reported for several species including *E. camaldulensis* (Grunwald and Karschon 1974), *E. grandis* (Reddy and Rockwood 1989) and *E. saligna* (Bowersox *et al.* 1990). However, few studies have examined the relationship between lignotuber development and coppice production.

This study aimed to determine the genetic control of coppicing and lignotuber development in *E. globulus* (*sensu* Brooker 2000) and their genetic interrelationship. We examine the patterns of natural genetic variation in these traits in families sampled throughout the geographic range of the species, and provide the first estimates of their heritability in *E. globulus*. We also report the genetic correlations amongst these regenerative traits and other economically important traits such as later age growth and wood density (MacDonald *et al.* 1997; Dutkowski and Potts 1999).

Materials and methods

Genetic material

The genetic control of coppicing was investigated by using a common environment field trial at Massy Greene in northern Tasmania (41°05′S, 145°54′E), while a glasshouse trial with families in common with the Massy Greene trial provided a comparison between coppice production and seedling lignotuber development. Both trials were established from a range-wide collection of open-pollinated seed of *E. globulus* and intergrade populations, undertaken by the CSIRO Australian Tree Seed Centre in 1987 and 1988 (Gardiner and Crawford 1987, 1988). Genetic material within the Massy Greene trial in northern Tasmania represented a subset of the material used in previous studies of the genetic variation in *E. globulus* (MacDonald *et al.*1997; Dutkowski and Potts 1999; Jordan *et al.* 1999, 2000). The *E. globulus* population was arranged in 23 subraces (modified from Dutkowski and Potts 1999), reflecting the geographic origins of parent trees (Table 1). As with previous studies (e.g. Dutkowski and Potts 1999), samples from Wilson's Promontory Lighthouse were excluded from the analysis owing to atypical shrublike growth.

Coppice trial

The Massy Greene *E. globulus* base population trial was established by North Forest Products (now Gunns Ltd) in 1989. The trial consisted of five replicates in a resolvable incomplete block design (further details of the trial design are given in Jordan *et al.* 1994). The trial was converted to a seed orchard in November 1998, but cut stumps of culled trees were allowed to coppice. Of the nearly 6000 trees in the original

Table 2. Traits measured, the transformation used, overall means and their units

References refer to previously published studies in which the results of analyses included data for that trait from the Massy Greene trial; *n* is the number of measurements for each trait; and mean is the back-transformed whole trial mean for each trait

Trait	Description and transformation	*n*	Mean
	Field trial (Massy Greene)		
P/A	Presence (1) or absence (0) of coppice	3562	0.67
Cheight (cm)	$(\text{cheight})^{0.85}$		
	Modal height of leaders coppicing from stump. Stumps not producing coppice were treated as missing values.	2443	85.6
Cstems	$(\text{cstems})^{0.32}$		
	Number of major stems coppicing from the stump, counted at the base of stems. Stumps not producing coppice were treated as missing values.	2442	15.5
Pilo (mm)	Pilodyn penetration at 5 years. One tree per plot in two replicates, the average of two measurements per tree. See MacDonald *et al.* 1997.	1392	13.2
Dbh (cm)	Diameter at 1.3 m over bark at 8 years	4693	19.8
Bark (mm)	$(\text{bark})^{0.71}$		
	Bark thickness, the average of two measurements. Only in four replicates. See Dutkowski and Potts 1999.	4409	7.7
	Glasshouse		
Noligno	Number of nodes with lignotubers at 1 year	374	0.8
Ligwidth (mm)	Width across lignotubers at the cotyledonary node after 1 year	528	8.4
Stemdiam (mm)	Stem diameter at the cotyledonary node after 1 year	528	6.8
Rligno	(ligwidth – stemdiam)/stemdiam	528	0.2

trial, 3594 living trees were felled and available for assessment of coppice production. Measurement of coppice production was undertaken 15 months after felling. A low percentage of stumps covered with slash from felling were excluded, leaving 3562 stumps for analysis (Table 2).

Three measurements of coppice production were taken from each stump after 15 months: presence or absence (P/A) of coppice shoots; modal height of the coppice shoots (cheight); and the number of coppice shoots produced per stump (cstems). Other traits previously assessed at Massy Greene were incorporated into this study for cross-correlation and comparison of relative levels of heritability. The additional traits included were diameter at breast height over bark prior to felling (dbh; 8 years); pilodyn penetration at 5 years (pilo) (Macdonald *et al.* 1997) and relative bark thickness at 4 years (bark) (Dutkowski and Potts 1999) (see Table 2). Pilodyn penetration is an indirect measure of wood density, with increased pilodyn penetration indicating decreased wood density (Greaves *et al.* 1996; Raymond and MacDonald 1998). For modal coppice height, the number of coppice stems and bark thickness, the regression of log(standard deviation) on log(mean) indicated that power transformations were required to standardise the variances (Box and Cox 1964). The transformations are shown in Table 2.

Lignotuber trial

Sixty-six families were common to both the Massy Greene and glasshouse trials, allowing estimation of genetic correlations between seedling lignotuber formation and coppice production. The glasshouse trial contained 550 plants in all, from 87 open-pollinated families with 1–16 plants per family. The trial comprised 19 randomised blocks with between 4 and 81 families present in any block and between one and three non-contiguous plants per family occurring in a block. The genetic material in the glasshouse trial was selected from 10 subraces with families representing the extremes of genetic variation in bark thickness within *E. globulus* (Dutkowski and Potts 1999). After 12 months, the number of nodes with lignotubers was counted (noligno) and width across lignotubers including the stem (ligwidth) and stem diameter at the cotyledonary node, perpendicular to the lignotubers (stemdiam) were measured. In order to account for growth, the size of lignotubers relative to stem diameter (rligno) was calculated according to Ladiges and Ashton (1974):

$$\text{rligno} = \frac{(\text{ligwidth} - \text{stemdiam})}{\text{stemdiam}}$$

Statistical procedures

ASReml (Gilmour *et al.* 1995, 2002) was used to conduct mixed model analyses of the trial data. Residual maximum likelihood estimates of variances, covariances and correlations uniquely attributable to genetic and design effects in the trials were obtained.

General linear mixed model

An individual tree model with subrace and replicate as fixed effects was used. The univariate model was defined as

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z_1 c} + \mathbf{Z_2 a} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of n observations for the dependent variable, β is the vector of fixed effects including subrace and the replicate term (in the respective trials), $\mathbf{c}$ is the vector of random incomplete block effects (only for the Massy Greene trial), $\mathbf{a}$ is the vector of random additive genetic effects and $\mathbf{e}$ is the vector of random residuals. $\mathbf{X}$, $\mathbf{Z_1}$ and $\mathbf{Z_2}$ are incidence matrices relating observations to factors in the model. The variance for each component is defined as

$$\text{Var}[c] = \mathbf{C} = \mathbf{I}\sigma_c^2,$$

$$\text{Var}[a] = \mathbf{G} = \mathbf{A}\sigma_a^2,$$

$$\text{Var}[e] = \mathbf{R} = \mathbf{I}\sigma_e^2,$$

where $\mathbf{A}$ is the numerator relationship matrix for the additive genetic effects and $\mathbf{C}$, $\mathbf{G}$ and $\mathbf{R}$ represent incomplete block, additive and residual covariance matrices between the observations, respectively.

The expected values and variances of the model are as follows:

$$\mathrm{E}\begin{bmatrix}\mathbf{y}\\ \mathbf{c}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{X\beta}\\ \mathbf{0}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix},\ \mathrm{Var}\begin{bmatrix}\mathbf{y}\\ \mathbf{c}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{V} & \mathbf{ZC} & \mathbf{ZG} & \mathbf{R}\\ \mathbf{CZ}' & \mathbf{C} & \mathbf{0} & \mathbf{0}\\ \mathbf{GZ}' & \mathbf{0} & \mathbf{G} & \mathbf{0}\\ \mathbf{R} & \mathbf{0} & \mathbf{0} & \mathbf{R}\end{bmatrix}$$

The phenotypic covariance matrix is:

$$\mathbf{V}=\mathbf{Z}_1\mathbf{C}\mathbf{Z}_1'+\mathbf{Z}_2\mathbf{G}\mathbf{Z}_2'+\mathbf{R}.$$

In bivariate analyses **y**, **c**, **a** and **e** consist of vectors containing observations for two traits so that

$$\mathbf{y}=(\mathbf{y}_1',\mathbf{y}_2'),\mathbf{c}=(\mathbf{c}_1',\mathbf{c}_2'),\mathbf{a}=(\mathbf{a}_1',\mathbf{a}_2'),\mathbf{e}=(\mathbf{e}_1',\mathbf{e}_2'),$$

$$\mathbf{X}=\mathbf{X}_1+\mathbf{X}_2,\mathbf{Z}_1=\mathbf{Z}_{1_1}+\mathbf{Z}_{1_2},\mathbf{Z}_2=\mathbf{Z}_{2_1}+\mathbf{Z}_{2_2},$$

$$\mathbf{C}=\mathbf{I}_c\times\mathbf{C}_o,\mathbf{R}=\mathbf{I}_N\times\mathbf{R}_o\ \text{and}\ \mathbf{G}=\mathbf{A}\times\mathbf{G}_o.$$

The variance–covariance matrices for the incomplete block, additive genetic effects and residuals are represented by $\mathbf{C_o}$, $\mathbf{G_o}$ and $\mathbf{R_o}$, respectively:

$$\mathbf{C}_o=\begin{bmatrix}\sigma^2_{c_1} & \sigma_{c_{12}}\\ \sigma_{c_{12}} & \sigma^2_{c_2}\end{bmatrix}\mathbf{G}_o=\begin{bmatrix}\sigma^2_{a_1} & \sigma_{a_{12}}\\ \sigma_{a_{12}} & \sigma^2_{e_2}\end{bmatrix}\text{and}\ \mathbf{R}_o=\begin{bmatrix}\sigma^2_{e_1} & \sigma_{e_{12}}\\ \sigma_{e_{12}} & \sigma^2_{e_2}\end{bmatrix}$$

OPAINV (Dutkowski *et al.* 2001), a Fortran program for use with ASReml, was employed to form the inverse of the relationship matrix accounting for 30% selfing in open-pollinated progeny (Griffin and Cotterill 1988).

Narrow-sense heritabilities were calculated in ASReml as:

$$h^2=\frac{\sigma^2_a}{\sigma^2_a+\sigma^2_e}.$$

The genetic correlation between an all-or-none trait and another normally distributed can be estimated without transformation so long as the incidence level of the all-or-none trait exceeds 10% (Olausson and Rönningen 1975). Thus, pairwise genetic correlations between the presence of coppice and other traits were calculated directly, as for quantitative traits. However, heritability of coppicing (based on presence/absence data) was estimated by using the general linear model with a probit link function. The significance of the heritability estimates and genetic correlations were tested with a *t*-test.

Least squares means for each subrace were estimated from the PREDICT statement in ASReml. Pilodyn penetration and bark thickness were not sampled in all replicates of the Massy Greene trial. In the case of cross-classified data with information absent in some cells, least squares means are not estimable from the PREDICT statement (Gilmour *et al.* 2002). Therefore, subrace least squares means for these variables were estimated by ignoring the effect of replicate. Pairwise (Pearson's) correlations between subrace least squares means were estimated by using PROC CORR in SAS Version 8 (SAS Institute, 1999).

Results and discussion

Variation between subraces

Normally *E. globulus* coppices vigorously (Jacobs 1979; Turnbull and Pryor 1984; Matthews 1992; Wirthensohn and Sedgley 1998), but only 67% of the trees in the Massy Greene trial produced coppice. Such low rates of coppicing contrast with the results of the coppicing trials conducted in Chile, where the success rate of coppicing in *E. globulus* was found to be about 93%, 14 months after felling (Prado *et al.* 1990; Alarcón 1994). This could be due to factors such as differences in genetic material or season of felling. The starch content of *E. obliqua* lignotubers shows significant seasonal variation (Cremer 1973). Coppice reproduction in eucalypts is reported to be maximal when trees are felled in late winter or spring and minimal when felled in summer (Blake 1983; Wirthensohn and Sedgley 1998). The Massy Greene trial was felled in November (late spring in Tasmania) and it is possible that the timing of felling was suboptimal for *E. globulus*.

There was significant variation between subraces in the presence of coppice and the number of stems produced but not in coppice height (Table 3, Fig. 1). The proportion of stumps coppicing ranged from 43 (Strzelecki Foothills) to 73% (Recherche Bay) at the subrace level (Table 4). The least squares means for coppice height at 14 months after felling ranged from 63 (Foothills) to 94 cm; however, Foothills and Dromedary were the only subraces with least squares mean for coppice height of less than 80 cm. Despite significant genetic correlations between the three measures of coppicing within subraces (r_g = 0.39–0.63; Table 5), the patterns of geographic variation at the subrace level were statistically independent (0.27–0.42: n.s.). There does not appear to be any geographic trend in the variation in coppice production on the basis of presence/absence data, with the exception of a west–east clinal trend across the Otway Ranges (39°S, 144°E, Fig. 1*a*). The trend follows a rainfall gradient (Dutkowski and Potts 1999) and parallels local clines in increasing bark thickness (Dutkowski and Potts 1999) and drought tolerance (Dutkowski 1995). Subraces from south-eastern Victoria, including those from the Strzelecki Ranges, produce fewer stems when coppicing than do subraces from the Furneaux group of islands and the Tasman Peninsula (Fig. 1*b*).

Significant variation occurred between subraces in the glasshouse trial for number of lignotubers, lignotuber width and relative size of lignotubers, but not seedling stem width (see Table 3). The number of nodes with lignotubers on a seedling ranged from zero to three over the period of the study (1 year). Lignotubers developed in every subrace studied; however, in the case of the Recherche Bay subrace, a mean of only 0.45 nodes had lignotubers per tree (Table 4) and only 33% of trees produced lignotubers (data not shown). The least squares means for relative lignotuber size ranged from 0.08 (Recherche Bay) to 0.53 (Eastern Otways) (Table 4 and Fig. 2*c*). There was strong genetic correlation between the three measures of lignotuber size both within (0.64–0.84) and between (0.95–0.97) subraces (Table 5). The most extensive lignotuber development could be found in the

Table 3. Variance components and narrow-sense heritabilities

For subrace, the denominator d.f. was taken to be equivalent to the residual d.f. in all cases. Incomplete block is shown as iblock. The number of subraces was used as the denominator d.f. in the case of replicate. The values for the variance components are based on the transformed variable. Replicate in the Massy Greene trial is not equivalent to replicate in the glasshouse trial. P/A is presence or absence of coppice; cheight is modal height of coppice leaders (cm); cstems is the number of stems coppicing from the stump; pilo is pilodyn penetration (5 years; mm); dbh is diameter at breast height (8 years; cm); bark is relative bark thickness (4 years); noligno is the number of nodes with lignotubers (1 year); stemdiam is diameter of the stem at the cotyledonary node (1 year; mm); ligwidth is the width across lignotubers at the cotyledonary node (1 year; mm); rligno is the lignotuber width relative to stem width as defined by Ladiges and Ashton (1974). Significance levels are based on F and T tests. n.s., not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

	Trait	Variance components			Fixed effects							
					Replicate		Between subraces		Within subraces			
		Iblock	Additive	Error	F_{rep}	$P > F$	$F_{subrace}$	$P > F$	h^2	s.e. (h^2)	t	$P >$ T
Field trial (Massy Greene)	P/A (probit)	0.06	0.07	1.00	23.33	***	2.03	**	0.07	0.03	2.36	*
	Cheight	5.91	29.69	151.08	12.37	***	1.36	n.s.	0.16	0.05	3.58	***
	Cstems	0.01	0.04	0.20	49.24	***	5.14	***	0.17	0.04	3.79	***
	Pilo	0.04	0.89	1.70	2.16	n.s.	9.56	***	0.34	0.09	3.97	***
	Dbh	0.16	8.06	16.97	3.42	**	7.88	***	0.32	0.04	8.84	***
	Bark	0.05	0.09	0.27	6.66	**	12.17	***	0.25	0.03	7.19	***
Glasshouse	Noligno		0.11	0.23	1.39	n.s.	4.93	***	0.31	0.11	2.67	**
	Stemdiam		0.54	0.64	5.30	**	1.44	n.s.	0.46	0.13	3.30	**
	Ligwidth		1.48	1.97	4.62	**	4.23	***	0.43	0.13	3.10	**
	Rligno		0.02	0.02	1.62	*	9.78	***	0.51	0.14	3.38	***

Table 4. Least squares means by subrace for all traits

Means for cheight, cstems and bark have been back transformed. P/A is presence or absence of coppice; cheight is modal height of coppice leaders; cstems is the number of stems coppicing from the stump; pilo is pilodyn penetration (5 years); dbh is diameter at breast height (8 years); height is tree height (4 years); bark is relative bark thickness (4 years); noligno is the number of nodes with lignotubers (1 year); stemdiam is diameter of the stem at the cotyledonary node (1 year); ligwidth is the width across lignotubers at the cotyledonary node(1 year); rligno is the lignotuber width relative to stem width as defined by Ladiges and Ashton (1974)

	Field trial (Massy Greene)						Glasshouse			
Subrace	P/A (probit)	Cstems	Cheight	Dbh (cm)	Pilo (mm)	Bark	Noligno	Ligwidth (mm)	Stemdiam (mm)	Rligno
Far Western Otways	0.55	17.70	94.05	18.60	15.16	7.54				
Western Otways	0.58	15.76	88.42	22.02	13.88	8.21				
Cape Patton	0.62	15.58	80.31	21.46	13.91	8.57				
Eastern Otways	0.68	15.35	86.15	20.45	13.32	8.75	1.33	10.44	6.84	0.53
Strzelecki Ranges	0.58	13.45	91.22	20.99	12.16	8.26	1.00	8.75	6.95	0.27
Strzelecki Foothills	0.43	12.25	86.93	21.98	12.65	8.19				
Gippsland Coastal Plain	0.54	11.09	87.44	21.36	13.86	7.47				
Gippsland Foothills	0.55	10.26	63.71	20.36	12.59	7.40				
Flinders Island	0.64	20.32	88.01	20.24	12.95	7.68				
Southern Furneaux	0.67	19.68	86.55	19.67	12.72	7.54	0.67	7.75	6.92	0.12
St Helens	0.69	16.84	87.57	19.07	13.83	8.66	0.78	8.46	6.44	0.31
North-eastern Tasmania	0.61	13.35	86.96	17.57	12.04	7.80	0.73	7.98	6.72	0.19
Inland north-eastern Tasmania	0.67	13.40	90.36	18.73	13.44	8.34	1.14	9.30	6.52	0.42
Dromedary	0.49	15.14	72.71	17.01	12.25	7.11				
South-eastern Tasmania	0.64	13.96	88.71	19.19	13.11	7.89				
Southern Tasmania	0.68	16.62	91.73	20.97	13.07	7.36	0.75	8.18	6.94	0.18
Tasman Peninsula	0.67	20.68	90.55	19.26	13.19	7.00				
Recherche Bay	0.73	15.78	84.72	19.20	12.10	7.46	0.45	6.76	6.25	0.08
Port Davey	0.51	15.21	88.88	16.86	13.33	6.20				
Western Tasmania	0.65	16.68	81.88	19.11	13.50	6.98	0.57	7.70	7.09	0.10
King Island	0.51	16.65	80.35	22.02	14.51	7.30	0.64	8.21	7.16	0.15

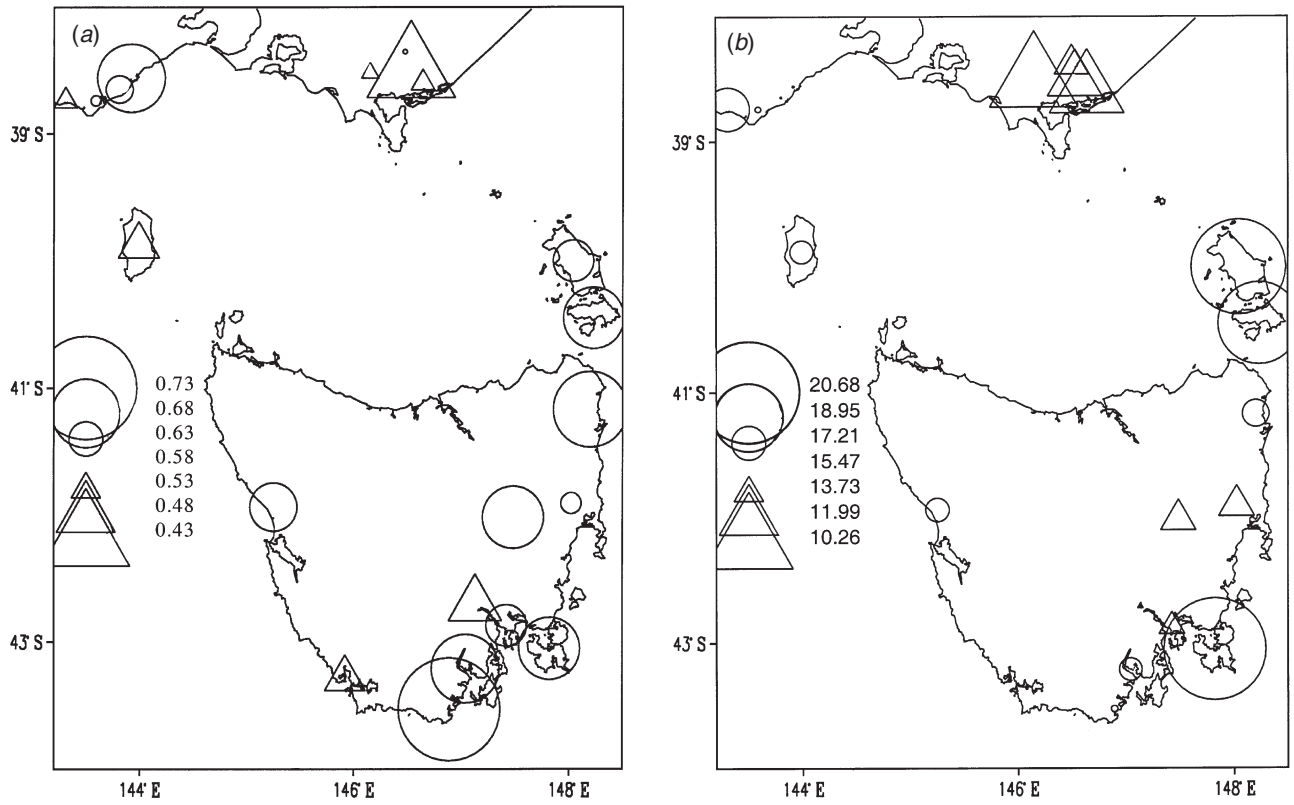

Fig. 1. Geographic variation in (*a*) the presence/absence of coppicing and (*b*) the number of stems coppicing from the stump. Circles represent higher rates of coppice reproduction and more stems; triangles represent lower rates of coppice reproduction and fewer stems in (*a*) and (*b*), respectively. The marker scale is centred on the range midpoint of the subrace least squares means values.

Eastern Otways subrace, with a mean of 1.33 nodes with lignotubers per tree and 92% of trees producing lignotubers. Western (Western Tasmania, King Island) and far south-eastern (Recherche, Southern Tasmania) Tasmanian subraces produced fewer lignotubers (Fig. 2*b*). These subraces exist in wetter environments and have thinner bark (Kelly 1997; Dutkowski and Potts 1999). The latter trend is reflected in the significant correlation between lignotuber traits and relative bark thickness at the subrace level (Table 5). This result is consistent with previous reports of eucalypt species or populations from drier environments having greater lignotuber development (Gill 1997). There is limited correlation between lignotuber traits and relative bark thickness within subraces (0.13–0.46, Table 5), indicating that parallel selection may be acting on these traits.

Variation within subraces

Significant genetic variation was found within subraces for all coppice and lignotuber traits investigated (Table 3). The heritability of coppice characteristics was reported to range from 0.45 to 0.71 in *E. grandis* (Reddy and Rockwood 1989). In the case of *E. globulus* the heritability of coppicing traits was the lowest of all traits measured. Heritabilities ranged from 0.07 for the presence of coppice, to 0.16 and 0.17, respectively, for modal coppice height and the number of coppice stems (Table 2). In contrast, lignotuber traits showed moderate heritability, ranging from 0.31 to 0.51, with relative lignotuber size the most heritable trait measured (Table 3). Other traits assessed in the field trial also exhibited moderate levels of heritability (h^2 = 0.21–0.34) and the heritability of variation in seedling stem diameter was the second highest (h^2 = 0.46) (Table 3). Despite extensive reports of heritability for growth and wood property traits (Lopez *et al.* 2002), these are the first estimates of heritability for coppice and lignotuber traits in the species.

Within subraces, the presence of coppice regeneration was positively genetically correlated with all traits measured in the Massy Greene trial, except for pilodyn penetration. No significant relationship was found between pilodyn penetration and coppice production, indicating that coppicing is genetically independent of wood density. Presence of coppice was significantly genetically correlated with tree size prior to felling (dbh *v.* P/A, r_g = 0.61; Table 5). However, there was little association of subsequent coppice growth with tree size prior to felling (dbh *v.* cstems, r_g = 0.26;

Table 5. Pairwise genetic (lower) and subrace (upper) correlations (Pearson's) for all traits

Genetic correlations with presence/absence (P/A) data were calculated without transformation to the probit scale. Statistically significant ($P < 0.05$) correlations are shown in bold. Correlations involving traits from the glasshouse trial are based on only 10 subraces; correlations between traits measured at the Massy Greene trial are based on 21 subraces. P/A is presence or absence of coppice; cheight is modal height of coppice leaders (cm); cstems is number of stems coppicing from the stump; pilo is pilodyn penetration (5 years; mm); dbh is diameter at breast height (8 years; cm); bark is relative bark thickness (4 years); noligno is the number of nodes with lignotubers (1 year); stemdiam is diameter of the stem at the cotyledonary node (1 year; mm); ligwidth is the width across lignotubers at the cotyledonary node (1 year; mm); rligno is the lignotuber width relative to stem width as defined by Ladiges and Ashton (1974)

	Field trial (Massey Greene)						Glasshouse			
	P/A	Cheight	Cstems	Dbh	Pilo	Bark	Noligno	Ligwidth	Stemdiam	Rligno
P/A		0.27	0.42	–0.11	–0.11	0.25	0	–0.08	**–0.69**	0.15
Cheight	**0.42**		0.36	0	0.24	0.16	0.48	0.31	–0.26	0.40
Cstems	**0.63**	**0.39**		–0.13	0.23	–0.17	–0.47	–0.35	0.24	–0.44
Dbh	**0.61**	0.12	**0.26**		0.24	**0.43**	0.12	0.21	0.57	0.01
Pilo	0.07	–0.04	–0.16	0.13		0.06	0.1	0.31	0.33	0.20
Bark	**0.33**	0.14	0.08	**0.57**	**0.25**		**0.79**	**0.75**	–0.41	**0.88**
Noligno	**0.66**	0.1	0.19	–0.34	**0.63**	0.13		**0.97**	0.03	**0.95**
Ligwidth	**0.89**	0.53	0.17	0.21	0.12	**0.46**	**0.77**		0.16	**0.95**
Stemdiam	**0.91**	0.49	–0.27	0.18	0.16	0.34	0.22	**0.64**		–0.18
Rligno	0.33	0.06	0.27	0.07	0.12	0.26	**0.84**	**0.66**	–0.15	

dbh *v.* cheight, $r_g = 0.12$; Table 5). This is consistent with previous reports that plant vigour prior to damage is a primary determinant of successful vegetative regeneration (Hillis and Brown 1978; Blake 1983; Noble 1984). However, the present study shows that this is only one of three mechanisms independently operating to determine the success of coppicing in *E. globulus*. Coppicing success is also strongly genetically correlated with seedling stem diameter (P/A *v.* stemdiam, $r_g = 0.91$) and less strongly correlated with the number of nodes with lignotubers (P/A *v.* noligno, $r_g = 0.66$). These two seedling traits are genetically independent of each other ($r_g = 0.22$: n.s.) and genetically independent of diameter at 8 years of age ($r_g = 0.18$: n.s., and $r_g = 0.21$: n.s., respectively). The genetic correlation between the presence of coppice and relative lignotuber size was not significant, and while there was a significant correlation between the presence of coppice and lignotuber width (P/A *v.* ligwidth, $r_g = 0.89$; Table 5), this was solely due to covariation with seedling stem diameter. For example, the genetic correlation between the presence of coppice and lignotuber width was only 0.37 when seedling stem diameter was included as a covariate and was not significantly different from zero. Similarly, the genetic correlation between relative bark thickness and the presence of coppice (bark *v.* P/A, $r_g = 0.33$) was not significant when dbh was included as a covariate (data not shown).

Lignotuber development has previously been suggested to enhance coppice production (Jacobs 1979; Webley *et al.* 1986; Bowersox *et al.* 1990; Noble 2001). The present study found the presence of coppice, and not subsequent coppice growth, to be correlated with lignotuber development in *E. globulus*. Bark thickness has no effect on coppice success at the age of 9 years, nor does wood density (as measured by pilodyn penetration; Table 5). Noble (2001) showed that lignotubers have an abundance of meristematic tissue available to differentiate into vegetative buds when the stem is damaged. The present study suggests that the probability of later-age coppicing in *E. globulus* is not affected by the relative size of this organ, but the number of seedling nodes producing the organ. However, the strongest determinant of coppice success appears to be not the lignotuber *per se*, but the size of the seedling stem at the cotyledonary node.

It is clear from other observations that lignotubers *per se* are not essential for successful coppicing and the two closely related species *E. grandis* and *E. saligna* are a case in point (Gill 1997). *E. grandis* tends not to have lignotubers while most *E. saligna* seedlings develop lignotubers (Burgess and Bell 1983), yet coppicing of both species is believed to be equivalent (Eldridge *et al.* 1993; Gill 1997). Broad swelling of the basal portion of the stem of seedlings rather than discrete lignotuberous organs occur in some eucalypts (e.g. *E. pilularis*) and this is also believed to enhance vegetative regeneration (Boland *et al.* 1984). While most of the internal wood is lignified, peripheral vascular tissues in lignotubers are known to function as sinks for carbohydrates and water (Noble 2001). It is possible that swollen stem bases in seedlings also act as carbohydrate sinks, thus providing nutrients for improved coppice production. Alternatively, the presence of a swollen seedling stem base or many lignotubers in *E. globulus* may reflect an increased density of epicormic meristem strands (as described by Burrows 2002) available to produce regenerative buds. In any case, the present study shows that these mechanisms are genetically independent, can co-occur in the same species (and potentially even in the same individual) and may represent primary storage and bud proliferation functions.

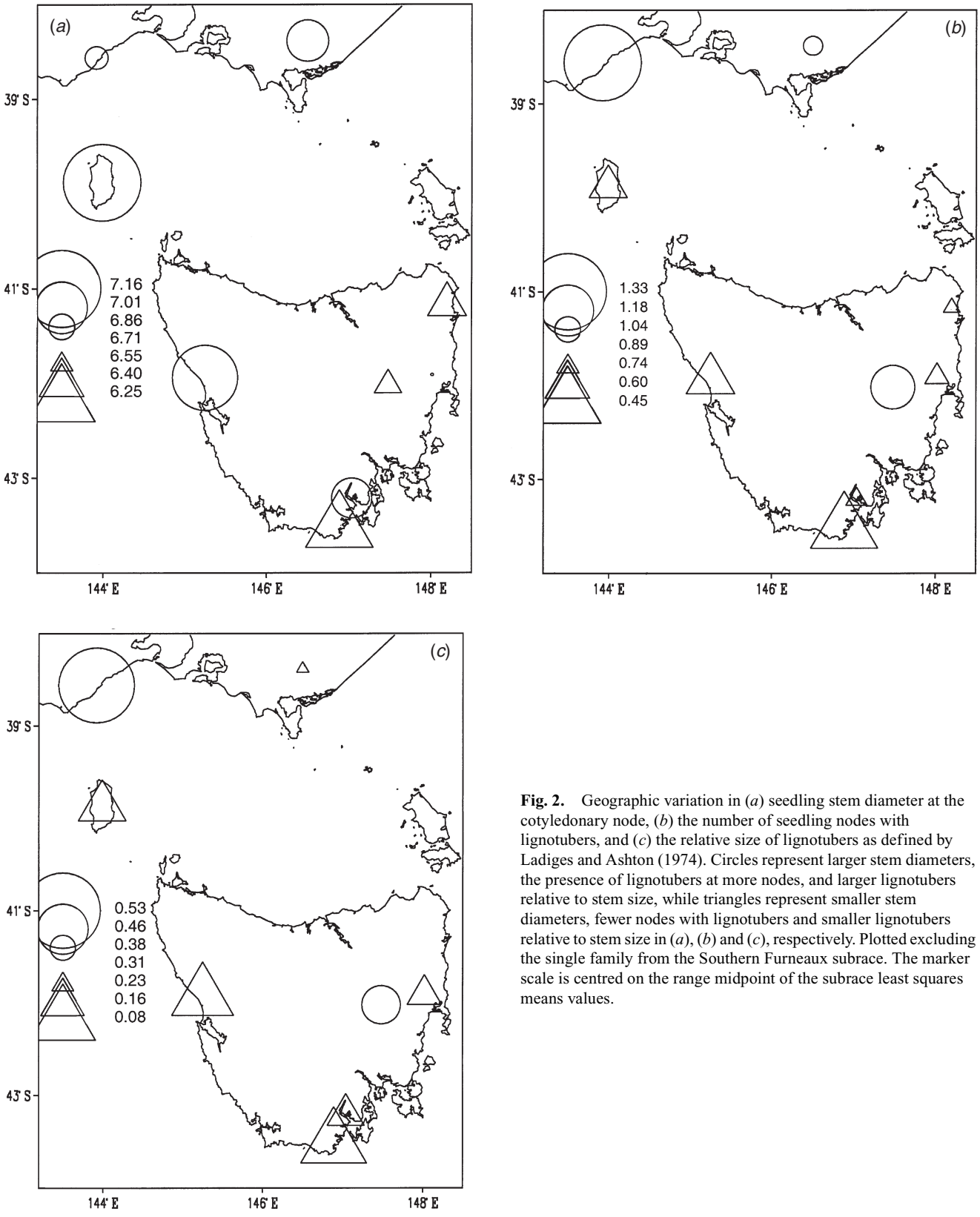

Fig. 2. Geographic variation in (*a*) seedling stem diameter at the cotyledonary node, (*b*) the number of seedling nodes with lignotubers, and (*c*) the relative size of lignotubers as defined by Ladiges and Ashton (1974). Circles represent larger stem diameters, the presence of lignotubers at more nodes, and larger lignotubers relative to stem size, while triangles represent smaller stem diameters, fewer nodes with lignotubers and smaller lignotubers relative to stem size in (*a*), (*b*) and (*c*), respectively. Plotted excluding the single family from the Southern Furneaux subrace. The marker scale is centred on the range midpoint of the subrace least squares means values.

Conclusions

There is significant genetic variation between and within subraces in their ability to reproduce by coppice and produce lignotubers, indicating both traits are amenable to artificial and natural selection. Further, seedling stem diameter and the number of seedling nodes with lignotubers appear to be indicators of the ability of a tree to produce coppice and may provide useful selection traits to improve the success of coppice regeneration. This quantitative genetic approach has argued for three independent genetically based mechanisms impacting on coppice success. The success of coppice production in *E. globulus* is dependent on tree vigour prior to felling, the number nodes with lignotubers in seedlings and finally the diameter of the stem at the cotyledonary node of seedlings.

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