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## The Genetic Control of Flowering Precocity in *Eucalyptus globulus* ssp. *globulus*

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### Abstract

The genetic control of flowering precocity was examined in 4 base population trials of *Eucalyptus globulus* ssp. *globulus* in Tasmania, which include nearly 600 open-pollinated families from 46 collection localities. Flowering precocity (measured as the presence/absence of capsules and/or flower buds at age 4) was found to be highly heritable ( $h^2_L = 0.47$  or  $0.59$ ; averaged across 3 or 4 trials respectively), and exhibit little genotype by environment interaction. Significant differences in the propensity for flowering precocity were observed between the 4 trials and also between different collecting localities. Progenies from localities on the Furneaux Group of islands showed significantly earlier flowering than those from other localities. Flowering precocity was generally not genetically correlated with growth (average  $r_g = 0.04$ ), indicating that selection for this trait alone would have little impact on early growth. In addition pre-

cocious flowering was not significantly correlated with pilodyn penetration (average  $r_g = -0.07$ ), although the consistent negative genetic correlation across 4 trials may be indicative of a weak positive genetic relationship with wood density. The potential of selecting for precocious flowering as a means of decreasing the generation interval in breeding programs is discussed.

*Key words:* REML, heritability, genetic correlation, generation interval, provenances, binomial traits.

*FDC:* 165.3; 181.521; 232.1; 176.1 *Eucalyptus globulus*; (946).

### Introduction

From a breeding perspective, the rate of incorporation of new genetic material into commercial planting stock depends on both the gains made per generation, and the rate of generation

turnover (NAMKOONG *et al.*, 1988). The generation interval is governed by the earliest age at which key traits can be reliably assessed and time to reproductive maturity. The age at which eucalypts first produce flowers varies markedly between species and individuals within a species (ELDRIDGE *et al.*, 1993). In the case of *Eucalyptus globulus*, studies of age-age correlations suggest selection for growth can be efficient as early as 4 years of age (BORRALHO *et al.*, 1992). However at this age, and particularly with canopy closure, only a small percentage of individuals will have reached reproductive maturity. First flowering of *Eucalyptus globulus* may occur as early as 5 years in fertilised plantations in Australia (GRIFFIN, 1989; GROSSMAN, 1990), but can be considerably longer in natural environments (HASAN and REID, 1995).

All trees propagated from seed have been described as undergoing a period of juvenility during which they will not flower or fruit with this aspect of juvenility setting a lower limit to the rate of generation turn-over (SEDGLEY and GRIFFIN, 1989; CHALUPKA and CECICH, 1997). However, the induction of flowering by artificial means has led to the view that juvenile trees are simply more reluctant to flower during the early years after planting rather than lack the ability to do so (LONGMAN, 1976). Treatment with the growth inhibitor paclobutrazol is now widely exploited as a means of stimulating flowering in *Eucalyptus*, and under specific glasshouse conditions flowering has been induced after only 19 months using *Eucalyptus globulus* (HASAN and REID, 1995). Nevertheless, there are considerable costs involved in the use of paclobutrazol. Furthermore, even if recalcitrant trees are treated directly in trials, there will be a further delay of at least one year before flowers are available and even then not all trees are responsive to such a treatment. Grafting and establishing selections into breeding arboreta or environments more conducive to flowering is also a common means of stimulating flowering (ELDRIDGE *et al.*, 1993). However, this procedure is again expensive and may also involve delays of 2 to 3 years before material can be used. Increase in yield through selection for heavy and precociously bearing genotypes is one of the major objectives for fruit tree breeders (JANIK and MOORE, 1975; ALSTON and SPEIGEL-ROY, 1985). Selection for precocious flowering has also been suggested as a means of reducing the generation interval in forest trees (GREENE and PORTERFIELD, 1962; PRYOR, 1966; GRIFFIN, 1989; CHALUPKA and CECICH, 1997). This can simply be achieved by only carrying forward trees which have reached reproductive maturity at the time of selection, although this could involve a loss of gain in other traits. The success of this strategy will depend on the level of genetic variation in flowering precocity in the population, and whether there are adverse genetic correlations with economically important traits in the breeding objective (HAINES and WOOLASTON, 1991). There is increasing evidence that the length of this juvenile phase or time to first flowering is under genetic control in other genera (GERHOLD, 1966; TEICH and HOLST, 1969; JEFFERS and NIENSTAEDT, 1972; SCHMIDTLING, 1981; ERIKSSON and JONSSON, 1986; CHALUPKA and CECICH, 1997). However, while there have been suggestions that precocious flowering is under genetic control in *Eucalyptus* (e.g. PRYOR, 1966; BOLOTIN, 1975; VANKATESH and SHARMA, 1976; WILTSHIRE *et al.*, 1992), no detailed quantitative studies have been published.

In the present study, we examine the genetic control of flowering precocity in 4 base population trials of *Eucalyptus globulus* ssp. *globulus* and examine the genetic correlations between flowering precocity and other key selection traits. Stem diameter and pilodyn penetration were used as indirect measures of tree volume and wood density, which have been

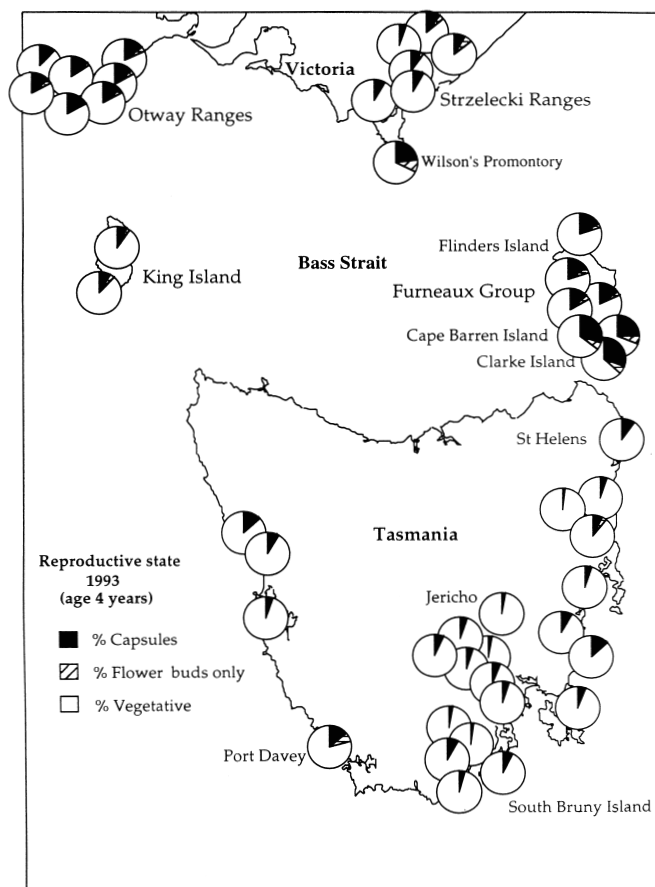


Figure 1. – Mean proportion of trees with capsules (flowered age 3), flower buds only (first flowering age 4) and those which were non-reproductive (at age 4) for 46 localities covering the entire natural range of *Eucalyptus globulus* ssp. *globulus* (see JORDAN *et al.*, 1994, for more information). Values were averaged over the 4 trial sites. The extent of precocious flowering in the Wilson's Promontory population has been underestimated, as most progeny from this locality were observed to have flower buds at age 2 or age 3, but many aborted due to the suppression of this uniquely shrub like form of *E. globulus* ssp. *globulus* in the trials.

identified as key traits in a breeding objective designed for kraft pulp production (see GREAVES *et al.*, 1997). The work presented extends other studies of genetic variation in flowering time (GORE and POTTS, 1995), growth (POTTS and JORDAN, 1994a; BORRALHO *et al.*, 1995) and wood density (MACDONALD *et al.*, 1997) in *E. globulus* ssp. *globulus*.

## Materials and Methods

### Genetic Material

The progenies studied were grown from a range wide collection of open-pollinated seeds of *Eucalyptus globulus* ssp. *globulus*, undertaken by the CSIRO Australian Tree Seed Centre in 1987 and 1988, as detailed in JORDAN *et al.*, (1995). This collection comprised nearly 600 open-pollinated seed lots, which were grouped into 46 collection localities (see JORDAN *et al.*, 1994; Figure 1). Two localities (Wilson's Promontory in Victoria and Port Davey in Western Tasmania), although shown in figure 1, were excluded from the genetic analysis as they were atypical (JORDAN *et al.*, 1994).

### Trial Sites, Design and Measurements

The 4 trials included in this study were established by North Forest Products in northern Tasmania. All trials contained 5 replicates, each with between 21 to 28 incomplete blocks

(using a resolvable incomplete block design, see PATTERSON and WILLIAMS, 1976) of 20 to 25 families in 2-tree contiguous plots (JORDAN *et al.*, 1995). A fifth trial (Woolnorth) was assessed for flowering but excluded from the analysis due to poor flowering (<1%). Flowering precocity was assessed as the presence/absence of capsules and/or flower buds at 4 years of age. Other measurements analysed include 4 year diameter at breast height (over bark) and pilodyn penetration. The pilodyn is a hand-held instrument which drives a high precision steel pin into a wood sample with known force (GREAVES *et al.*, 1995), providing an indirect measure of wood density. The pilodyn penetration was recorded on half the trees (1 tree per plot and 2 measurements averaged per tree), in 2 of the 5 replicates at each site at age 5. Pilodyn and diameter data used is detailed in MACDONALD *et al.* (1997).

### Statistical Analysis

For each trial, estimates of variance and covariance components and associated heritabilities of flowering precocity, and correlations between this trait and diameter or pilodyn penetration were obtained by Restricted Maximum Likelihood methods (REML), using VCE REML (GROENEVELD, 1996), with the following model:

$$y = \mu + Xb + Zf + Tl + e \quad (1)$$

where  $y$  is the vector of  $N$  observations for flowering precocity, diameter or pilodyn penetration;  $b$  is the vector for the replicate within trial effect (assumed fixed);  $l$  is the vector for the locality effect (assumed random), and  $f$  is the vector for the family (or GCA) effects.  $X$ ,  $T$  and  $Z$  are incidence matrices for the fixed and random effects respectively. The expected mean and variances of the parameters  $y$ ,  $b$ ,  $f$ ,  $l$  and  $e$  are as follows:

(2)

$$E \begin{bmatrix} y \\ e \\ l \\ f \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}, \quad \text{Var} \begin{bmatrix} y \\ e \\ l \\ f \end{bmatrix} = \begin{bmatrix} V & R & TG_l & ZG_f \\ R & R & 0 & 0 \\ G_l T' & 0 & G_l & 0 \\ G_f Z' & 0 & 0 & G_f \end{bmatrix}$$

where:

$$V = R + ZG_f Z' + TG_l T'$$

$$R = \sum_{j=1}^m R_{oj}, \text{ with } m = \text{number of records,}$$

$$G_l = I_l \otimes G_{ol}$$

$$G_f = I_f \otimes G_{of}$$

and:

$G_{of}$  = variance-covariance matrix for the family effect,

$G_{ol}$  = variance-covariance matrix for the locality effect,

$R_{oj}$  = residual covariance matrix for tree  $j$ ,

$\otimes$  = Kronecker product,

$\oplus$  = direct sum.

Narrow-sense heritability estimates were calculated as:

$$h_{0/1}^2 = \frac{2.5 V_f}{V_f + V_e} \quad (3)$$

where  $h_{0/1}^2$  is the heritability on the observed binomial scale,  $V_f$  is the variance for the family (GCA) effects, and  $V_e$  is the error variance. This follows adjustments made for related mating in open-pollinated sibs in previous studies (e.g. VOLKER

*et al.*, 1990; and HODGE *et al.*, 1996) and assumes the average relationship amongst sibs is  $\frac{1}{2.5}$ , equating to a selfing rate of approximately 30% (GRIFFIN and COTTERILL, 1987). Standard errors for heritabilities on the observed binomial scale follow BECKER (1984). Because heritability estimates obtained from the analysis of flowering precocity ( $h_{0/1}^2$ ) were on a binomial scale, they were converted to an underlying 'liability' scale (equation 3) for comparison across trials as detailed in CHAMBERS *et al.* (1996). This conversion is necessary because on the binomial scale variances differ according to the mean (MCGUIRK, 1989):

$$h_L^2 = h_{0/1}^2 \frac{p(1-p)}{z^2} \quad (4)$$

where  $h_{0/1}^2$  is the heritability on the observed binomial scale,  $h_L^2$  is the heritability for flowering precocity on the 'liability' scale,  $p$  is the incidence of flowering in the trial, and  $z$  is the height of the ordinate at the threshold corresponding to the incidence in that trial.

Genetic correlations were calculated as:

$$r_G = \frac{\text{cov}(f_x, f_y)}{\sqrt{V_{f_x} \cdot V_{f_y}}} \quad (5)$$

where  $r_G$  is the genetic correlation between traits  $x$  and  $y$ , and  $\text{cov}(f_x, f_y)$  is the covariance between family effects for trait  $x$  and  $y$ . Although genetic correlations between binomial and normally distributed traits are equivalent on the binomial and underlying liability scales (OLAUSON and RÖNNINGEN, 1975), phenotypic correlations must be adjusted to the liability scale for comparison across trials (following CHAMBERS *et al.*, 1996). Phenotypic correlations between flowering precocity and diameter or pilodyn penetration were calculated from:

$$r_L = r_{0/1} \cdot \left[ \frac{p_{fp}(1-p_{fp})}{z_{fp}^2} \right]^{\frac{1}{2}} \quad (6)$$

$r_L$  and  $r_{0/1}$  are the phenotypic correlations between flowering precocity and diameter or pilodyn penetration calculated on the liability and binomial scale respectively,  $p_{fp}$  is the incidence of precocious flowering, and  $z_{fp}$  is the height of the threshold on the liability scale for flowering precocity (following OLAUSON and RÖNNINGEN, 1975). Approximate standard errors for genetic correlations were calculated following FALCONER and MACKAY (1996):

$$\sigma_{r_G} = \frac{(1-r_G^2)}{\sqrt{2}} \sqrt{\frac{\sigma_{h_x^2} \sigma_{h_y^2}}{h_x^2 h_y^2}} \quad (7)$$

$\sigma$  denotes standard error.

Locality correlations were calculated from:

$$r_l = \frac{\text{cov}(l_x, l_y)}{\sqrt{V_{l_x} \cdot V_{l_y}}} \quad (8)$$

$r_l$  is the correlation between localities for traits  $x$  and  $y$ , and  $\text{cov}(l_x, l_y)$  is the covariance between locality effects of traits  $x$  and  $y$ .

The significance of locality and trial by locality effects were examined using likelihood ratio statistics (SHAW, 1987; MCCULLAGH and NELDER, 1989) in which data from all trials was pooled according to the following model:

$$y = Su + Xb + Za + Tl + Wp + e \quad (9)$$

$u$  is the vector for the trial effect (assumed fixed),  $p$  is the vector for the trial\*locality interaction effects (assumed random), and  $S$  and  $W$  are incidence matrices for the trial and trial\*locality effects respectively. The comparison of likelihoods between the models in this case assumes that the pooled data is not distributed significantly different from a normal distribution.

## Results

### Overall Means

Trial means and standard deviations for flowering precocity, diameter growth and pilodyn penetration are listed in *table 1*. The proportion of trees having reached reproductive maturity by age 4 was generally low (*Table 1*) but differed significantly between trials ( $p < 0.001$ ), ranging from only 1% at Woolnorth to 25% at Massy Greene. Apart from the early flowering of the Lighthouse locality, few flower buds were apparent in these trials prior to three years of age. Capsules recorded on trees at the 4 year assessment therefore resulted mainly from flowering at age 3. The proportion of trees with capsules range from <1.0% at Woolnorth to 24% at Massy Greene (*Table 1*) indi-

cating that most of the precocious flowering had occurred at age 3 with little recruitment at age 4. At the trial mean level, there was a trend for the most precocious trials (Massy Greene and West Ridgley) to be the faster growing and to have greater pilodyn penetration (hence lower wood density).

### Variance Components and Heritabilities

Variance components of flowering precocity due to family (GCA), locality and residual effects, and individual heritability estimates on both the binomial scale ( $h^2_{0/1}$ ), and the adjusted underlying liability estimate ( $h^2_L$ ), are shown in *table 2*. On the binomial scale the locality variance accounted for 2.7% to 10.1% and the family variance estimate accounted for 8.4% to 10.9% of the total variation. Estimates of heritability for flowering precocity ( $h^2_L$ ), were moderate to high, ranging from 0.45 at Massy Greene to > 1 at Exeter, and averaged 0.59 across all 4 trials. The higher estimate at Exeter is almost certainly a consequence of an upward bias in the liability adjustment caused by the low incidence of flowering (2%) (see MERCER and HILL, 1984). If this trial is excluded, the heritabilities for flowering precocity across the remaining 3 trials is still moderate to high, averaging 0.47.

Differences between localities were highly significant ( $p < 0.001$ ), and consistent across trials with non significant

*Table 1.* – Overall trial means for flowering precocity (proportion), diameter and pilodyn at Woolnorth, West Ridgley, Massy Greene, Latrobe and Exeter, in northern Tasmania.

Traits	Woolnorth	West Ridgley	Massy Greene	Latrobe	Exeter
<b>Flowering Precocity</b>					
<b>(Capsules and Flower Buds)</b>					
No. parents	474	431	568	546	529
No. records	4427	3893	5436	5063	5090
Mean	0.01	0.16	0.25	0.12	0.02
s.d.	0.07	0.36	0.44	0.32	0.14
<b>(Capsules only)</b>					
Mean	0.00	0.13	0.24	0.06	0.02
s.d.	0.06	0.30	0.43	0.28	0.14
<b>Diameter</b>					
<b>(cm)</b>					
No. parents	474	431	568	546	529
No. records	4427	3893	4965 *	5063	5090
Mean	7.67	10.94	12.94	6.61	6.98
s.d.	2.59	3.10	3.37	1.94	2.15
<b>Pilodyn</b>					
<b>(mm)</b>					
No. parents	456	411	553	529	514
No. records	1261	1105	1498	1440	1432
Mean	12.26	13.81	13.44	11.83	12.75
s.d.	1.71	1.80	1.89	1.59	1.68

\*) abnormal growth phenotypes (runts, double stemmed and damaged plants) excluded

Table 2. – Mean flowering (in % units) and estimates of locality ( $V_{local}$ ), family ( $V_f$ ), error ( $V_e$ ), and total phenotypic ( $V_{total}$ ) variances (% of total phenotypic shown in parentheses) and corresponding heritability (standard error shown in parentheses) on the binomial scale ( $h^2_{0/1}$ ) in the 4 trials. Also shown are heritabilities for the family (GCA) effect ( $h^2_{0/1}$ ;  $2.5 * V_f / (V_f + V_e)$ ) adjusted to the liability scale ( $h^2_L$ ) for flowering precocity at age 4 years.

Trial	% Flower	$V_{local}$	$V_f$	$V_e$	$V_{total}$	$h^2_{0/1}$ (s.e.)	$h^2_{op}$
West Ridgley	15.67	0.0039 (4.2)	0.0092 (10.0)	0.0790 (85.8)	0.0921	0.21 (0.03)	0.48
Massy Greene	25.39	0.0106 (10.1)	0.0114 (10.9)	0.0830 (79.0)	0.1050	0.24 (0.02)	0.45
Latrobe	12.40	0.0057 (6.9)	0.0070 (8.4)	0.0705 (84.7)	0.0832	0.18 (0.03)	0.47
Exeter	2.00	0.0005 (2.7)	0.0017 (9.2)	0.0163 (88.1)	0.0185	0.19 (0.02)	>1

trial\*locality effects ( $0.10 < p < 0.05$ ). Locality effects were mainly due to the high proportion of precocious flowering in progenies from localities on the Furneaux Group of islands, particularly Clarke and Cape Barren Islands (Figure 1). Flowering occurred at very low frequencies in localities from eastern Tasmania, with localities from the Otway Range region intermediate between these and the Furneaux Group localities. The 2 atypical populations, Lighthouse and Port Davey were amongst the most precocious localities sampled.

#### Correlation Between Sites for Flowering Precocity

The locality (Table 3a) and genetic (Table 3b) correlations between flowering precocity in different trials were generally high, averaging 0.86 and 0.60 respectively. These high correlations suggest that there is little genotype by environment interaction and flowering precocity can be considered as a single trait across trials, at least at the locality level. The lowest genetic correlation was between the Massy Greene and Exeter trials (0.40), however the locality correlation between these 2 trials was high (0.80).

#### Correlations Between Flowering Precocity, Diameter and Pilodyn Penetration

The locality, genetic and phenotypic correlations of flowering precocity with diameter and pilodyn penetration are given in

Table 3. – Estimates of the locality ( $r_l$ ) and additive genetic ( $r_g$ ), correlations between flowering precocity at the different trials.

#### a) Locality Correlations ( $r_l$ ) $\pm$ s.e.

Trial	Massy Greene	Latrobe	Exeter
West Ridgley	0.96 (0.03)	0.92 (0.05)	0.82 (0.07)
Massy Greene	-	0.95 (0.03)	0.80 (0.07)
Latrobe		-	0.72 (0.09)

#### b) Genetic Correlations ( $r_g$ ) $\pm$ s.e.

Trial	Massy Greene	Latrobe	Exeter
West Ridgley	0.76 (0.03)	0.69 (0.05)	0.64 (0.06)
Massy Greene	-	0.54 (0.06)	0.40 (0.06)
Latrobe		-	0.59 (0.05)

table 4. The genetic correlations between diameter and precocious flowering were low, averaging 0.04 across the 4 trials, while the phenotypic correlations were consistently positive, averaging 0.63. There were negative additive genetic ( $r_g = -0.16$ ) and locality ( $r_l = -0.30$ ) correlations between flowering precocity and diameter at Latrobe. At this site, precocious flowering is genetically related with slower growth, both within and across localities. However, this was not the case in other trials where these correlations were positive, but only significantly different from zero at West Ridgley. Thus precocious flowering localities at West Ridgley also exhibit the fastest growth, the opposite of what appears to be occurring at Latrobe.

The within locality genetic correlations between flowering precocity and pilodyn penetration (Table 4) were consistently negative (average  $r_g = -0.07$  across all trials), but not significantly different from zero. Phenotypic correlations ranged from  $-0.53$  at Latrobe to  $0.11$  at Massy Greene and averaged  $-0.19$  across all sites. The between locality genetic correlations were variable and averaged  $-0.21$  across all trials. However, this correlation was only significant at Latrobe where precocious flowering localities also tended to have lower pilodyn penetration. These results indicate that the genetic relationship between flowering precocity and pilodyn penetration is low, but there is a slight tendency for precocious flowering to be genetically associated with decreased pilodyn penetration (thus higher wood densities).

#### Discussion

The present study clearly indicates that flowering precocity in *E. globulus* ssp. *globulus* is highly heritable, and exhibits little genotype-by-environment interaction. Flowering precocity appears to be under stronger genetic control than other traits examined across these same trials (e.g. growth 0.2, BORRALHO *et al.*, 1995; survival 0.3, CHAMBERS *et al.*, 1996; pilodyn 0.4, McDONALD *et al.*, 1997). Studies on seasonal flowering time in this species have also yielded high heritability estimates (GORE and POTTS, 1995), suggesting that reproductive traits in particular are under strong additive genetic control, consistent with their taxonomic importance in the genus. As the heritability estimates were derived from open-pollinated progenies, where the male parent is unknown, the degree of non-additive variation can not be assessed. It is now well established that the genetic parameters estimated from open-pollinated material of *E. globulus* are biased due to differential

Table 4.— Estimates of locality ( $r_l$ ), additive genetic ( $r_g$ ) and phenotypic correlations ( $r_p$ ), of flowering precocity with diameter and pilodyn penetration, across 4 trials. Correlations differing from zero by more than 2 standard errors (s.e.) are considered significant.

Trial	Diameter			Pilodyn Penetration		
	$r_l$	$r_g$	$r_p$	$r_l$	$r_g$	$r_p$
	locality (s.e.)	genetic (s.e.)	total	locality (s.e.)	genetic (s.e.)	total
West Ridgley	0.40 (0.14)	0.16 (0.06)	0.71	0.08 (0.15)	-0.08 (0.09)	-0.37
Massy Greene	0.12 (0.13)	0.11 (0.06)	0.58	0.02 (0.13)	-0.08 (0.08)	0.11
Latrobe	-0.30 (0.16)	-0.16 (0.07)	0.56	-0.63 (0.09)	-0.15 (0.09)	-0.53
Exeter	0.04 (0.17)	0.04 (0.06)	0.65	-0.13 (0.14)	-0.02 (0.08)	-0.06

inbreeding, particularly for growth (HARDNER and POTTS, 1995; HODGE *et al.*, 1996). However the parameter estimates reported in this study are likely to be relatively accurate as inbreeding has been demonstrated not to have a significant effect on precocious flowering in either *E. globulus* (HARDNER and POTTS, 1995) or *E. nitens* (HARDNER and TIBBITS, 1997). The strong inheritance of this trait is supported by crosses between precocious and late flowering forms of a closely related taxa *E. maidenii* reported by PRYOR (1966). In this case the crosses between a selected precocious flowering tree and a tree which would normally not flower until 5 to 6 years resulted in progeny which also flowered early.

Significant differences in the propensity for flowering precocity were observed between localities of *E. globulus* ssp. *globulus* in the present study. Genetic differences between provenances in flowering precocity have been reported in *E. occidentalis* (BOLOTIN, 1975) and *E. gunnii* (POTTS, 1985). In the latter case, POTTS suggests high fire frequency has resulted in the selection for precocious flowering in a mallee population of *E. gunnii*. In the present case, early flowering appears to be occurring in the Furneaux Group of islands which are among the driest localities sampled (see POTTS and JORDAN, 1994a). It is also well established that *E. globulus* plants from an exposed coastal headland on Wilson's Promontory (data excluded from this analysis, but shown in Figure 1) also exhibit precocious flowering as well as precocious transition to adult foliage (HASAN and REID, 1995; POTTS and JORDAN, 1994b), characteristics suggested by HASAN (1993) to have evolved in response to the harsh environment at this site. In the present case it is difficult to determine whether the precocious flowering has been directly or indirectly selected at these localities. Earlier flowering localities of *E. globulus* also tend to undergo earlier vegetative phase change (e.g. Furneaux Islands, Wilson's Promontory; G. JORDAN, unpubl. data). However PRYOR (1966) and WILTSHIRE *et al.* (1992) suggest that vegetative and reproductive phase change are independent in eucalypts which would argue that any association of these traits at the locality level is the result of independent selection.

It is generally concluded that there is antagonism between vegetative growth and flowering at the genetic level for a range of plants (ROMBERGER, 1967; BROWNING, 1985; GRIFFIN, 1989; CHALUPKA and CECICH, 1997). However precocious flowering tends to be phenotypically associated with faster early growth in many species (CHALUPKA and CECICH, 1997),

consistent with the present results. With the exception of SCHMIDTLING (1981), GRIFFIN (1989) notes that there is little quantitative information on the genetic association between flowering precocity and growth in the forestry literature. In the present study the sign of the genetic correlations between flowering precocity and growth varied between trials, and on average there was little tendency for genes for early flowering to be associated with genes affecting growth. This generally weak genetic correlation indicates that (at least within localities), selection based on flowering precocity alone would generally not impact genetically on early growth. However, when genetic correlations were calculated for the presence of only flower buds at age 4 years, there was a consistent negative additive genetic correlation in all trials (-0.06 to -0.18; average -0.12; unpubl. data). A large proportion of the trees with flower buds at age 4 years also flowered the previous year, suggesting that it may take several years of flowering before growth is adversely affected. It is thus possible that the deleterious effects of early flowering on subsequent growth will amplify this effect in latter years, as SCHMIDTLING (1981) showed for loblolly pine. It appears from the consistently positive phenotypic correlation between the 2 traits that some forms of environmental treatment aimed at improving growth rate may also indirectly improve flowering precocity at the phenotypic level. Evidence for this comes from the often large discrepancy between the genetic and phenotypic correlations, suggesting that error correlations are also expected to be strongly positive. In other words, positive residuals in growth lead to positive residuals for flowering, indicating that enhancing growing conditions (up to 3 years of age) is likely to result in early flowering. This suggestion is also consistent with the tendency for faster growing trials to flower earlier.

The consistently negative genetic correlation between early flowering and pilodyn penetration may reflect a complex pleiotropic inter-relationship between growth rate, wood density and flowering. Increased growth rate has also been demonstrated to be genetically correlated with decreased wood density in this species (MACDONALD *et al.*, 1997). The pilodyn measures were taken 1 year later than diameter and an antagonistic effect of flowering on later growth can not be discounted. However, the same group of growth hormones, gibberellins, are known to affect both wood properties (ALONI and ZIMMERMAN, 1983) and influence flowering (HASAN and REID, 1995) and the possibility of genes affecting the bio-

synthesis, or inactivation of specific growth hormones, having a pleiotropic effect on precocious flowering and wood density can not be dismissed.

The capture of genetic gains made from a breeding population involves selecting the elite genotypes, as defined by the breeding objective, and then the propagation of these genotypes to generate commercial planting stock and a new breeding population (NAMKOONG *et al.*, 1988). The propagation strategy relies on a successful reproduction phase (HAINES and WOOLASTON, 1991). If the proportion of genotypes available for propagation (say those genotypes which have flowered) is not at an acceptable level, there will be 2 problems for a tree breeder to consider. Firstly, to carry out selections using only those genotypes which have flowered successfully, effectively introduces another stage of selection into both the breeding and deployment populations. The success of this strategy relies, ultimately, on the genetic relationship between precocious flowering and other key selection traits at selection age. Alternatively, the program could wait for all selected trees to flower. This could, however, seriously impede the rate of genetic progress in the breeding program for these key selection traits, by increasing the generation interval. Developing early selection techniques for economically important growth and wood traits, such as marker-aided selection, will be of little benefit if this type of approach is used as generation times will still be large.

While it has long been established that the induction of precocious flowering in seedlings would be of great benefit to breeding programs in *E. globulus* (PRYOR, 1966), the widely exploited artificial growth inhibitor paclobutrazol has only been used on a commercial basis for a handful of years. Paclobutrazol acts by inhibiting the oxidation of gibberellin precursors (HEDDEN and GRAEBE, 1985), and has been demonstrated as having an adverse relationship with vegetative growth (HETHERINGTON and JONES, 1990; HASAN and REID, 1995). The high heritabilities reported in this study for flowering precocity and generally insignificant genetic correlations with growth and wood density at this early age, show that an alternative to paclobutrazol treatment may be to make strong, direct selections on flowering precocity in the first few generations and attempt to bring the age of first selection and flowering into synchrony. Indeed, these results suggest that selections for increased wood density, as suggested by GREAVES *et al.* (1996) for eucalypt kraft pulp production would, if anything, indirectly select for precocious flowering. Although such a strategy has been proposed (PRYOR, 1966; GRIFFIN, 1989), a potential problem with this approach is that the proportion of trees to be selected in a breeding program tends to be fixed, and hence the addition of this trait as a selection criterion will effectively lower the selection pressure which can be applied to other economic traits (GODDARD, 1981; HAINES and WOOLASTON, 1991). This approach however must be weighed against the potential decrease in generation times and management costs of inducing flowering, with the value of such a strategy in terms of gains and costs per generation requiring careful consideration. In addition, the inclusion of genes for precocious flowering into a breeding population for timber or kraft pulp production may be undesirable in the long term, if the continuing expression of this trait in successive generations leads to significantly reduced wood yields due to the energy loss involved in wasteful flower and fruit production (GREENWOOD, 1987). However, in the case of *Eucalyptus* grown in short rotation plantations, flowering is naturally inhibited after canopy closure (usually around 4 to 5 years) due to intense competition.

## Conclusion

The results showed that precocious flowering of *Eucalyptus globulus* ssp. *globulus* was under a high degree of genetic control, with heritabilities ranging between 0.41 and 1.0. However, there were significant differences for flowering precocity between trials, indicating that favourable environmental conditions are important for the promotion of early flowering. Significant differences between progeny established from different localities was also shown, with localities from the Furneaux Group of islands showing significantly earlier flowering than other localities from the Tasmanian and Victorian mainlands. The performance of these localities was consistent across the 4 trials (i.e. there was no significant genotype by environment interaction).

Genetic correlations between flowering precocity and early growth were consistently low, ranging from -0.16 to 0.16, indicating that precocious flowering and growth are relatively independent at this age. The genetic correlations between precocity and pilodyn penetration were low and negative ranging from -0.02 to -0.15, indicating a slight tendency for precocious flowering genotypes to also have denser wood. Individual selections for flowering precocity would be greatly complicated due to the significant locality differences, and the potential to use this trait as a means of turning over generations for selection for other key selection traits (for example growth and wood density) would require careful consideration. However, the heritability of flowering precocity is high enough to allow quick gains to be made in this trait, and the negative correlation with growth low enough at age 4 to make this an interesting alternative to decrease the generation interval. However, this genetic relationship is likely to become more antagonistic with age, as the full impact of flowering is shown in the tree.

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