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A comparison of genetic information from open-pollinated and control-pollinated progeny tests in two eucalypt species

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Abstract Genetic-parameter estimates and parental breeding-value predictions were compared from open-pollinated and control-pollinated progeny populations of *Eucalyptus globulus* and two populations of *E. nitens*. For *E. globulus* there were two types of open-pollinated populations (native stand open-pollinated and seed orchard open-pollinated) and two types of control-pollinated populations (intra-provenance and inter-provenance full-sib families). For *E. nitens* there were two populations, a seed orchard open-pollinated population and intra-provenance full-sib families. Progeny tests were established across multiple sites and 2-year height and diameter were measured and volume calculated. Genetic parameters from native stand open-pollinated *E. globulus* were unlike the parameters from the other three *E. globulus* populations; heritability estimates were severely inflated, presumably due to high levels, and possibly differential levels, of inbreeding depression relative to the other populations. Estimates of dominance variance in the *E. globulus* full-sib populations were high, but were zero in the *E. nitens* population. Correlations among parental breeding values, predicted using data from the different populations, were generally low and non-significant, with two exceptions: predictions from the two *E. globulus* full-sib populations were significantly correlated ($r = 0.54$, $P = 0.001$), as were predictions from the *E. nitens* seed orchard OP and full-sib population ($r = 0.61$, $P = 0.08$). There was some indication that superior parents of *E. globulus* native stand open-pollinated families also tended to have above-average breeding values based on the performance of intra-provenance full-sib offspring. The consequences of these results for exploitation of base-population collections from native stands are discussed.

Key words Heritability · Dominance · Genotype × environment interaction · Inbreeding · *Eucalyptus*

Introduction

There are approximately 500 species in the genus *Eucalyptus* and between 20 and 30 of these have been widely planted. Two species which play important roles in commercial plantation forestry are *E. globulus* and *E. nitens*, both of which are adapted to cool temperate regions. *E. globulus* is one of the most widely planted eucalypts in the world, with significant plantation programs in Spain, Portugal, Italy, Chile, India, China, and Australia (Volker and Orme 1988). There is increasing interest in planting *E. nitens* in many of these same regions, particularly in areas where frosts are too harsh for optimum growth of *E. globulus*.

Despite the extensive use of various eucalypts around the world in plantation forestry, estimates of genetic parameters for eucalyptus species are not abundant in the scientific literature. Most of the estimates which are available are based on progeny tests planted at only one site with open-pollinated material collected from parent trees growing in native stands. The use of open-pollinated progeny tests to estimate genetic parameters involves assuming that families are true half-sib families (i.e., crosses are based on a large number of unrelated males and with no inbreeding (Borrahlo 1994). However, these assumptions are likely to be unrealistic for insect-pollinated species such as *Eucalyptus*, particularly in native stands. The degree to which these assump-

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tions are not met will affect the utility of both genetic-parameter estimates and breeding-value predictions developed from open-pollinated progeny tests. This problem is particularly relevant to the exploitation of base populations and it is important to identify the genetic bias involved in selection and the estimation of genetic parameters from such material (Potts and Jordan 1994). The purpose of this paper is to compare genetic parameters and breeding-value predictions from 2-year-old open-pollinated and control-pollinated progeny tests in two eucalyptus species, *E. globulus* and *E. nitens*, planted at multiple sites in Australia. Both of these species are in the early phases of domestication and most breeding programs are at the stage of exploiting material directly from native stands or land races (Eldridge et al. 1993).

Materials and methods

Genetic material

Ten *E. nitens* parents from the Toorongo provenance provided both full-sib and open-pollinated material. Open-pollinated seed from eight of the ten parents was collected from a seed orchard (containing selections from a number of provenances) and for two of the ten parents from a commercial plantation (presumably derived from a commercial collection within a single provenance). The same ten parents were also mated in a half-diallel design. Both open-pollinated and full-sib seed were then planted in progeny tests on four sites: Bega, Flynn, Hampshire, and West Ridgely, all in northwest Tasmania.

A total of 34 *E. globulus* parents from three provenances were included in the study in a factorial mating design (Fig. 1). A total of 20 parents from the Taranna provenance were mated in an intra-provenance factorial of 16 males × 4 females. A total of 13 parents from the King Island provenance were mated in an intra-provenance factorial of 10 males × 3 females. Inter-provenance factorials were also formed by crossing the 16 Taranna males × 3 King Island females, and crossing the 10 King Island males × 4 Taranna females. A total of 25 additional inter-provenance crosses were made, crossing the 15 Taranna males and the 10 King Island males to one female from South Flinders Island (see Volker and Orme 1988 for location details).

In addition to the different types of full-sib *E. globulus* families, families representing two types of open-pollinations (orchard and native stand) were included in the study. The 15 Taranna and 10 King Island parents used as males in the factorials were parent trees in native stands, and open-pollinated seed from these 25 trees was collected. All parents used as females in the factorials were included in a *E. globulus* seed orchard, where seed from those nine trees was collected. This seed orchard contained 35 families from 14 provenances of *E. globlulus* (see Volker et al. 1990).

Full-sib and open-pollinated families were planted together at six sites: (1) Bega, New South Wales, (2) Flynn, Victoria, (3) Parkham,

Fig. 1 Mating designs for four *E. globulus* populations (inter-provenance full-sib, intra-provenance full-sib, native stand open-pollinated, and seed orchard open-pollinated) and two *E. nitens* populations (intra-provenance full-sib and seed orchard open-pollinated). The numbers in the table represent the number of field locations in which a family is tested

E. globulus

CP Females (also females for seed orchard OP families)		CP Males (also females for native stand OP families)																										Seed Orchard OP
		Taranna																King Island										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
King Island	a	5	3	5	2	5	5	5	5	5	5	5	5	5		5	5	4	3	5	5	5	5	5	5	5	5	5
	b	5	1	5	5	2	2	5	5	5	5	3	3	5	3	5	4	5	5		5	2	5	2	5	5	5	4
	c	1	1				5	5	3	1	1	1	1	1	1	2	2	1	5	3	2		5	4	5	3	5	5
South Flinders	d	1	1		1	1	3	2	1	1	2	4	1	5	1	1	2	2	4	5	3	2	4	3	5	3	5	5
Taranna	e	1	3	3			1	2	1	5		3	2		1	1	2		1		2							2
	f	5	2	5	2	5	5	5	2	5	4	4	5	2	4	1	5	1							1		1	5
	g	5	5	2	5	5	5	5	5	5	5	5	5	5	4	5	2	5	1	1	4	1		2	1	1		5
	h	5	1	4	4		5	4	2		2	5	2	4	4		3		3	5	4	5				2		5
Native Stand OP		2	5		1	4	5	2	4	4	5	5	4	5	2	5	5	5	1	5	1	5	5	5	5	5	5	

E. nitens

Females	Males										Seed Orchard OP
	i	j	k	l	m	n	o	p	q	r	
i			2	1	3	4	4	2	1	3	4
j			2	1	2	3	4	2	4		4
k				2	1	3	4	1	1	4	4
l					3	2	3	4	1		4
m						4	3		4	1	4
n				1			4	2	3	1	3
o								2	4	1	4
p										1	4
q											4

Tasmania, (4) Hampshire, Tasmania, (5) West Ridgely, Tasmania, and (56) Manjimup, Western Australia. The distribution of families at these sites is shown in Fig. 1 and Table 1. Throughout the remainder of the manuscript, the following notation will be used to refer to the different populations:

GOP = *E. globulus* open-pollinated progeny from trees in native stands,
GSOP = *E. globulus* open-pollinated progeny from ramets in seed orchards,
G × GC = Intra-provenance full-sib *E. globulus* crosses ("close" crosses),
G × GW = Inter-provenance full-sib *E. globulus* crosses ("wide" crosses),
NSOP = *E. nitens* open-pollinated progeny from ramets in seed orchards, and
N × NC = Intra-provenance full-sib *E. nitens* crosses.

Field design and measurements

All sites were planted using an alpha-lattice design (Patterson and Williams 1976). Tree volume (dm^3) was estimated using diameter at breast height (1.3 m) over bark and total tree height (h) measured at 2 or 3 years (see Table 1) using the following formula:

$$\text{volume} = 1.3\pi(d/2)^2 + 1/3\pi(d/2)^2(h - 1.3)$$

Analyses were done for height diameter and volume. Results for all three variables were essentially identical, so only results for volume are presented.

Parameter estimation

All analyses to estimate variance components from the *E. globulus* factorials and open-pollinated tests were conducted with restricted maximum likelihood (REML) using SAS PROC VARCOMP (SAS 1990). It is not possible to specify the diallel-model structure in PROC VARCOMP due to the fact that parents are used as both males and females. Thus, all analyses to estimate variance components for the *E. nitens* diallels and open-pollinated tests were conducted with REML using GAREML (Huber 1993).

Open-pollinated data. The linear model used to represent open-pollinated data for a trait at a single site is:

$$y_{hijkl} = \mu + e_h + r_i + b_{ij} + f_k + fe_{hk} + p_{hijk} + w_{hijkl}$$

where

μ = a fixed general mean,
e_h = random effect of h^{th} environment, $h = 1, 2, \ldots e$,
$E(t_i) = 0$, $\mathrm{Var}(t_i) = \sigma_r^2$,
r_i = random effect of i^{th} environment, $i = 1, 2, \ldots r$,
$E(t_i) = 0$, $\mathrm{Var}(t_i) = \sigma_r^2$,
b_{ij} = random effect of j^{th} block within the i^{th} replication, $j = 1, 2, \ldots b$,
$E(r_{ij}) = 0$, $\mathrm{Var}(r_{ij}) = \sigma_b^2$,
f_k = random effect of k^{th} family, $k = 1, 2, \ldots d$,
$E(f_k) = 0$, $\mathrm{Var}(f_k) = \sigma_f^2$,
fe_{hk} = random effect of the interaction of the h^{th} environment and k^{th} family,
$E(f_k) = 0$, $\mathrm{Var}(f_k) = \sigma_f^2$,
p_{hijk} = random plot error of k^{th} family in the j^{th} block, i^{th} replication, h^{th} environment,
$E(p_{hijk}) = 0$, $\mathrm{Var}(p_{hijk}) = \sigma_p^2$,

w_{hijkl} = random tree error of l^{th} tree in $ijkh^{th}$ plot, $l = 1, 2, \ldots n$,
$E(w_{hijkl}) = 0$, $\mathrm{Var}(w_{hijkl}) = \sigma_w^2$, and
the covariances between all pairs of factors are assumed to be zero.

The f_k effects are assumed to be random and are associated with the average genetic effects of the open-pollinated families planted in each test. When open-pollinated families are considered as true half-sib families, and assuming no epistatic effects, f_k is the general combining ability of the k^{th} parent, so f_k is equal to 1/2 of the breeding value (BV) of the k^{th} parent. Thus, if an open-pollinated family is a true half-sib family, $\mathrm{Var}(f_k) = \sigma_f^2 = \mathrm{Var}(1/2\mathrm{BV}) = 1/4\sigma_A^2$ (i.e., 1/4 of the additive genetic variance). In other words, the coefficient of relationship (r) among half-sib progeny is 0.25. Open-pollinated families of *Eucalyptus* species are unlikely to be true half-sib families because of the high probability of both selfing and related matings. Eucalypts have a mixed mating system (both selfing and outcrossing) with an average outcrossing rate in native stands of around 78% (Moran and Bell 1983). Outcrossing rates in seed orchards may be higher, with one estimate of 90% for a *E. regnans* orchard (Moran et al. 1989). In addition, it is likely that many OP progeny from native eucalypt stands will exhibit "neighborhood inbreeding" due to short pollen dispersal distances associated with insect-vectored pollen, coupled with limited seed dispersal (Potts 1990). Complicating the use of OP progeny for genetic parameter estimates is the possibility that both the rate of selfing/related matings and inbreeding depression due to selfing/related matings can vary from family to family (Griffin and Cotterill 1988). Since it is difficult to evaluate how these factors might affect covariances among OP siblings, different authors have used a number of different coefficients of relationship ranging from 0.25 to 0.54 (Table 2). With a given coefficient of relationship (r), estimates of σ_A^2 and σ_{AE}^2 equal σ_f^2/r and σ_{fe}^2/r, respectively. Following the approach

Table 1 Location of trial sites, establishment and measurement dates, trial design and number of families in each cross type

Design	Site					
	Bega NSW	Flynn VIC	Parkham TAS	Hampshire TAS	W. Ridgely TAS	Manjimup WA
Latitude	36°36′	38°18′	41°26′	41°15′	41°09′	34°12′
Longtitude	149°46′	149°41′	146°37′	145°45′	145°46′	116°1′
Altitude	120m	170m	205M	470m	185m	240m
Established	8/90	7/90	8/90	7/90	7/90	7/90
Measured	5/92	6/92	8/92	8/92	8/92	3/93
Replicates	4	4	4	4	4	7
Inc. blocks/rep	10	11	13	7	15	11
Plots/block	14	18	14	9	20	11
Trees/plot	5	5	5	5	5	3
Cross type	Number of families in each cross type					
GOP	19	21	22	0	24	18
GSOP	6	7	8	0	8	7
G × GC	48	62	76	0	83	53
G × GW	33	49	58	0	85	37
NSOP	9	9	8	9	9	0
N × NC	18	32	0	14	35	0

Table 2 Heritability estimates for growth traits in some eucalyptus species

Author-date	Species	Cross type	r[a]	Trait[b]	Age (yrs)	h^2	Genetic material and comments
Kedharnath and Vakshasya 1978	*tereticornis*	OP	0.25	Ht	2	0.17	$n = 15$ from Indian plantation stands, one site
				Ht	4	0.25	
Kedharnath 1982	*grandis*	OP	0.25	Ht	2.5	0.20	$n = 13$ from Indian plantation stands, one site
				Ht	4.5	0.34	
Griffin and Cotterill 1988	*regnans*	OP	0.40	Ht	2.5	0.41	$n = 13$ from trees in two native stands stands, one site
				Vol	2.5	0.53	
				Ht	3.75	0.43	
				Vol	3.75	0.45	
		Outcross	Not appl.	Ht	2.5	0.19	$n = 13$ parents from two native stands, crossed in two factorials (within stand), one site
				Vol	4	0.22	
				Ht	2.5	0.18	
				Vol	4	0.18	
Woolaston et al. 1991b	*globulus*	OP	0.54	Dbh	4	0.10	$n = 20$ from native stands, combined 4-site analysis, little G × E
Woolaston et al. 1991a	*nitens*	OP	0.54	Dbh	4	0.21	$n = 94$ from native stands, 6 provenances, combined 3-site analysis, very little G × E
Borrahlo et al. 1992	*globulus*	OP	0.33	Sa	4	0.17	$n = 20$ from three Portuguese plantation stands, one site
				Sa	8	0.16	
				Sa	3	0.15	$n = 23$ from native stands in 5 provenances, plus $n = 20$ from California plantation stands, one site
				Sa	6	0.15	
				Sa	4	0.19	$n = 27$ from clonal seed orchard in Portugal, one site
				Sa	8	0.16	
Volker et al. 1992	*globulus*	OP	0.40	Ht	6	0.12	$n = 45$ from native stands, 14 provenances, one site
				Vol	6	0.19	
Whiteman et al. 1992	*nitens*	OP	0.40	Ht	9	0.23	$n = 32$ from native stands, one site
				Dbh	9	0.18	

[a] Coefficient of relationship assumed for open-pollinated progeny

[b] Dbh = diameter at breast height, Ht = height, Sa = sectional area, Vol = volume

used by Squillace (1974) and Cameron and Cotterill (1989), and assuming a selfing rate of 25% (Moran and Bell 1983) and 20 local males, one can derive a coefficient of relationship for OP families from native stands of 0.50. We will assume that $r = 0.5$ for the GOP population and, for convenience, also use $r = 0.5$ for the GSOP and NSOP populations in this study.

Full-sib data. The linear model used to represent factorial full-sib data for a trait was:

$$y_{hijklm} = \mu + e_h + r_i + b_{ij} + f_k + m_i + fm_{kl} + fe_{hk}$$
$$+ me_{hl} + fme_{hkl} + p_{hijkl} + w_{hijklm}$$

where

μ = a fixed general mean,

e_h = random effect of h^{th} environment, $h = 1, 2, \ldots e$,
$E(t_i) = 0$, $\text{Var}(t_i) = \sigma_r^2$,

r_i = random effect of i^{th} environment, $i = 1, 2, \ldots r$,
$E(t_i) = 0$, $\text{Var}(t_i) = \sigma_r^2$,

b_{ij} = random effect of j^{th} block within the i^{th} replication, $j = 1, 2, \ldots b$,
$E(r_{ij}) = 0$, $\text{Var}(r_{ij}) = \sigma_b^2$,

f_k = random effect of k^{th} female, $k = 1, 2, \ldots d$,
$E(f_k) = 0$, $\text{Var}(f_k) = \sigma_f^2$,

m_i = random effect of l^{th} male, $l = 1, 2, \ldots d$,
$E(f_k) = 0$, $\text{Var}(m_i) = \sigma_f^2$,

fm_{kl} = random effect of the interaction of the k^{th} female and l^{th} male,
$E(fm_{kl}) = 0$, $\text{Var}(fm_{kl}) = \sigma_s^2$,

fe_{hk} = random effect of the interaction of the h^{th} environment and k^{th} female,
$E(f_k) = 0$, $\text{Var}(f_k) = \sigma_{fe}^2$,

me_{hk} = random effect of the interaction of the h^{th} environment and m^{th} male,
$E(f_k) = 0$, $\text{Var}(f_k) = \sigma_{fe}^2$

fme_{hkl} = random effect of the interaction of the h^{th} environment and kl^{th} family,
$E(f_k) = 0$, $\text{Var}(f_k) = \sigma_{se}^2$,

p_{hijkl} = random plot error of kl^{th} family in the j^{th} block, i^{th} replication, h^{th} environment,
$E(p_{hijkl}) = 0$, $\text{Var}(p_{hijkl}) = \sigma_p^2$,

w_{hijklm} = random tree error of m^{th} tree in $ijklh^{\text{th}}$ plot, $l = 1, 2, \ldots n$,
$E(w_{hijklm}) = 0$, $\text{Var}(w_{hijklm}) = \sigma_w^2$, and

the covariances between all pairs of factors are assumed to be zero.

The linear model used to represent the diallel full-sib data is conceptually identical to the above model with one exception. GAREML will not handle all three of the terms *tests*, *reps*(*tests*), and *blocks*(*reps*) in the same model. Thus it was necessary to analyze the *E. nitens* data as a standard randomized complete block design, and disregard the incomplete blocks within reps.

For the full-sib factorial model, the variance associated with the f_k and m_l effects represents $1/4\sigma_A^2$, and similarly the variance associated with the fe_{hk} and me_{hl} effects represents $1/4\sigma_{AE}^2$ (i.e., 1/4 of the additive × environment interaction variance. Estimates of σ_A^2 and σ_{AE}^2 were then obtained as four-times the weighted averages of the male and female variance components, and male × environment and female × environment variance components. Additionally, the variance associated with fm_{kl} and fme_{hkl} effects represent $1/2\sigma_D^2$ and $1/2\sigma_{DE}^2$ (i.e., 1/2 dominance variance and dominance × environment variance, respectively).

Single-site and cross-site analyses. Prior to a combined analysis across sites, single-site analyses were conducted for all cross types in both species using individual tree data as the units of observation. This was done primarily to estimate within-plot variance (σ_w^2) at each site. To eliminate problems arising from site-to-site heterogeneity of variance, all measurements for a given site were divided by the within-plot standard deviation at that site. Similar transformations have been suggested as the most practical way to deal with the heterogeneity of variance in dairy breeding applications. If heterogeneous variance structures are ignored, parameter estimates can be affected, and there will some loss in selection efficiency (Visscher et al. 1991). Combined analyses across sites were then done using plot means as the unit of observation. Plot variances (σ_p^2) were then estimated from the error variances from the plot-mean analysis using the known within-plot variances and the harmonic mean of the number of trees per plot (Stonecypher 1992).

The genetic parameters estimated were heritability (h^2), Type-B genetic correlation (r_{Bg}) and, for full-sib data, the proportion of dominance variance (d^2) as follows: $h^2 = \sigma_A^2/\sigma_p^2$, where σ_p^2 = total phenotypic variance; $r_{Bg} = \sigma_A^2/\sigma_{AE}^2$; and $d^2 = \sigma_D^2/\sigma_p^2$. The Type-B genetic correlation is a measure of genotype × environment interaction (Burdon 1977); it ranges between 0 and 1, where 1 represents perfect correspondence of genotypes across environments, i.e., zero genotype × environment interaction. Both SAS VARCOMP REML and GAREML calculate estimates of variances and covariances of the variance-component estimates for each effect in the linear model. Standard-error estimates of estimates of the genetic-variance components σ_A^2, σ_{AE}^2, and σ_D^2 were then easily calculated as linear combinations of model-variance components. Standard errors of estimates of h^2 and d^2 were calculated following Dickerson (1969), with the assumption that σ_p^2 was constant. Standard-error estimates for r_{bg} were calculated according to the formula for the variance of a ratio (Namkoong 1979, p 232).

Inbreeding depression

For each site, the degree of inbreeding depression observed in the different populations was calculated. For both species, the growth of "inbred" populations relative to outcrossed populations was assumed to represent inbreeding depression. For *E. globulus*, the G × GW population would not be expected to exhibit any inbreeding depression since it resulted from controlled full-sib crosses among parents from different provenances. Thus, inbreeding depression of the GOP, GSOP, and G × GC populations were calculated relative to the G × GW population as

$$ID = [(A - B)/A] \times 100\%$$

where A = the G × GW mean and B = the GOP, GSOP or G × GC mean. Similarly, for *E. nitens*, the inbreeding depression of the NSOP was calculated relative to the N × NC population.

Prediction of breeding values

Breeding values for both *E. globulus* and *E. nitens* were predicted using GAREML with family means as the unit of observation. First, the GENSTAT REML directive (Lawes Agricultural Trust 1987) was used to calculate the weighted least square means for families (treating family as a fixed effect, and using individual tree data as the unit of observation) thus correcting for different rep and incomplete block effects. Next, these least square means were used in GAREML to predict breeding values both across sites and for each single site. Pearson's correlations between predicted parental breeding values developed from different progeny material were then examined.

Results and discussion

Within-plot variance

As might be expected, there was a strong relationship between mean site volume and within-plot variance (σ_w^2) at that site (Fig. 2). This relationship was quite striking for *E. globulus*, and is also apparent for *E. nitens*. For the

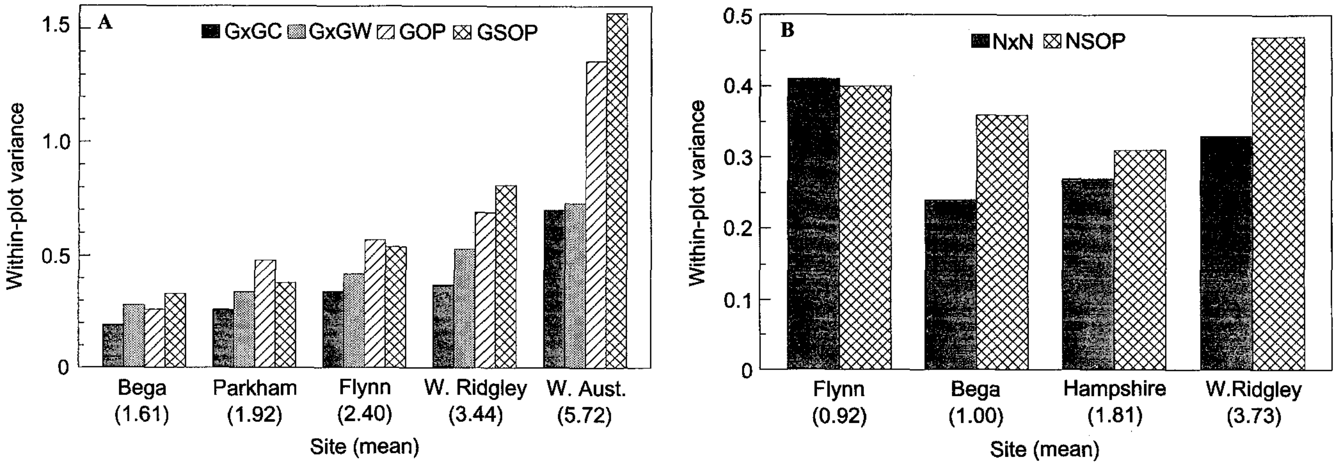

Fig. 2 A,B Within-plot variance for (**A**) four *E. globulus* populations and (**B**) two *E. nitens* populations at a number of field sites. The population abbreviations are:
GOP = *E. globulus* open-pollinated progeny from trees in native stands,
GSOP = *E. globulus* open-pollinated progeny from trees in seed orchards,
G × GC = Intra-provenance full-sib *E. globulus* crosses ("close" crosses),
G × GW = Inter-provenance full-sib *E. globulus* crosses ("wide" crosses),
NSOP = *E. nitens* open-pollinated progeny from trees in seed orchards, and
N × NC = Intra-provenance full-sib *E. nitens* crosses.
Site means are across all populations and are in units of dm^3

E. globulus populations, there was roughly a four-fold variation in σ_w^2 from the smallest to the largest site. Even discounting the West Australia site (which was a 3-year measurement), there was still roughly a two-fold variation. Variability in σ_w^2 for the *E. nitens* data was of slightly lower magnitude: the range of σ_w^2 was 0.24 to 0.41 for the N × NC, and 0.31 to 0.47 for the NSOP, tests. Thus, some sort of transformation of these data before a cross-site analysis would appear to justified.

In both *E. globulus* and *E. nitens* there were consistent differences in σ_w^2 among populations (Fig. 2). For *E. globulus*, the populations tended to rank as follows at each site, from smallest to largest σ_w^2: G × GC < G × GW < GOP < GSOP. For *E. nitens*, σ_w^2 from the NSOP population was usually larger than that from the N × NC population. Assuming that there is no inbreeding depression, σ_w^2 for open-pollinated populations will contain some genetic variance that is not present in σ_w^2 for controlled cross full-sib populations (approximately 1/4 of the additive variance plus 1/2 of the dominance variance); however, these effects should be small. Increases in σ_w^2 observed in open-pollinated versus control-pollinated populations have been attributed to an increase in the frequency of selfed progeny, which can often exhibit severe inbreeding depression (e.g., Sorenson and White 1987; Hardner and Potts 1995 a). This would explain the general trend that all OP populations show a higher σ_w^2 than do full-sib populations. It was interesting, however, to note that the GSOP population tended to have a higher σ_w^2 than the GOP population. The GOP population would be expected to exhibit some neighborhood inbreeding effects (from related matings) as well as effects of selfing, and thus one might expect more inflation of σ_w^2 from the presence of additional inbreds in the progeny. In a similar manner, one might expect a higher σ_w^2 in the G × GC than the G × GW populations due to the presence of inbreds from some related matings. Neither of these effects was observed. Intra-provenance crossing (G × GC and GOP) yielded a lower σ_w^2 than inter-provenance crossing (G × GW and GSOP, since the seed orchard contained selections from many provenances) for both the open-pollinated populations and the full-sib populations.

Single-site heritabilities

Although there were strong differences in volume heritability estimates from site-to-site for a given population, these effects were not consistent across populations. For example, at the West Ridgley site GOP had the highest h^2 estimate and G × GW the lowest, while at the Flynn site G × GW had the highest h^2 estimate and GSOP the lowest. Single-site heritabilities for GOP ranged from 0.00 at Bega to 0.53 at West Ridgley, and averaged 0.26 across the five sites. Similar, although somewhat lower, estimates were obtained by Borrahlo et al. (1992) and Volker et al. (1990) with older *E. globulus* material at single-sites (see Table 2). Note that these authors' estimates are lower despite assuming lower coefficients of relationship (Table 2). GOP h^2 estimates (average = 0.26) were generally higher than estimates from the seed orchard population, GSOP (average $h^2 = 0.10$), and the estimates from the full-sib populations, G × GC and G × GW (average $h^2 = 0.16$ and 0.10, respectively), even when using $r = 0.5$ (Table 3). Similar results were obtained by Griffin and Cotterill (1988) in that OP progeny from native stands yielded h^2 estimates roughly twice those calculated from full-sib data in *E. regnans*. For the *E. nitens* populations, average single-site h^2 for the NSOP population was 0.25, and for the N × NC population was 0.15. There was no trend for increasing heritability with increasing site mean for any of the *E. globlulus* populations, or for the N × NC population; however, the NSOP population did show this trend. Whiteman et al. (1992) reported a similar heritability for 9-year-old *nitens* from a native stand open-pollinated population ($h^2 = 0.23$).

Cross-site analyses

For *E. globulus*, genetic parameters estimated from the GSOP, G × GC and G × GW populations were generally similar (Table 4). Heritability estimates were low (h^2 from 0.02 to 0.08), r_{Bg} estimates ranged from 0.21 to 0.54 (thus genotype × environment interaction is high), and the proportion of dominance was high relative to the h^2 estimates (d^2 from 0.05 to 0.15). However, parameters estimated from the GOP population were strikingly different than the other three populations, with $h^2 = 0.33$ and $r_{Bg} = 1$, i.e. zero genotype × environment interaction. Inbreeding depression was present in small amounts in the G × GC and GSOP populations, 4 and 5%, respectively, but was quite substantial (17%) in the GOP population.

There was a striking similarity between the parameter estimates from the GSOP and the G × GW populations (Table 4, see also Table 3), with h^2 estimates of 0.02 in both populations and r_{Bg} estimates of 0.21 and 0.29. Since the *E. globulus* seed orchard had selections from a number of provenances, most of the out-crossed progeny were probably the result of inter-provenance crosses. This may account for the similarity with the estimates from the G × GW population (inter-provenance full-sib crosses).

For *E. nitens*, genetic parameters estimated from the NSOP population and the N × NC population were reasonably similar (Table 4), with relatively low h^2 estimates (0.09 and 0.05, respectively), and moderately low r_{Bg} estimates (0.47 and 0.39, respectively). No dominance variance was detected in the N × NC population, and there was essentially no inbreeding depression (1%). The low h^2 and high genotype × environment interaction observed in this study are substantially different from the results obtained by Woolaston et al. (1991 b)

Table 3 Estimates of heritability (h^2)[a], and means ($\bar{x}$) for 2-year-old volume from single-site analyses for different populations of *E. globulus* and *E. nitens* progeny. Conic volume is measured in units of dm^3

Pop'n[b]	Parameter	Site						
		Bega	Parkham	Flynn	Hampshire	W. Ridgley	W. Aust.	Average
GOP	h^2	0.00	0.18	0.30		0.53	0.27	0.26
	$\bar{x}$	1.32	1.48	1.88		2.97	5.33	
GSOP	h^2	0.10	0.11	0.00		0.00	0.27	0.10
	$\bar{x}$	1.65	1.66	2.28		3.17	5.66	
G x GC	h^2	0.15	0.12	0.14		0.23	0.16	0.16
	$\bar{x}$	1.64	1.79	2.22		3.33	5.48	
G x GW	h^2	0.14	0.04	0.18		0.04	0.12	0.10
	$\bar{x}$	1.61	1.92	2.40		3.44	5.72	
NSOP	h^2	0.28		0.07	0.29	0.37		0.25
	$\bar{x}$	1.09		0.82	1.81	3.64		
N x NC	h^2	0.12		0.16	0.10	0.23		0.15
	$\bar{x}$	1.00		0.92	1.81	3.73		

[a] Heritabilities estimated from single-site analyses are biased upwards by the presence of additive x environment interaction variance in the numerator (Comstock and Moll 1963; Hodge and White 1992). However, heritability estimates in the literature for *Eucalyptus* spp. are predominantly single-site estimates

[b] Population GOP = *E. globulus* open-pollinated progeny from trees in native stands,

GSOP = *E. globulus* open-pollinated progeny from trees in seed orchads,

G x GC = Intra-provenance full-sib *E. globulus* crosses ("close" crosses),

G x GW = Inter-provenance full-sib *E. globulus* crosses ("wide" crosses),

NSOP = *E. nitens* open-pollinated progeny from trees in seed orchards, and

N x NC = Intra-provenance full-sib *E. nitens* crosses

Table 4 Estimates of heritability (h^2), type-B genetic correlation (r_{Bg}), and proportion of dominance variance (d^2) and inbreeding depression (ID) for 2-year-old volume from cross-site analyses for different populations of *E. globulus* and *E. nitens*

Pop'n[a]	$h^2 \pm$ SE	$r_{Bg} \pm$ SE	$d^2 \pm$ SE	ID(%) ± SE
GOP	0.33 ± 0.15	1.00 ± na[b]		17 ± 3
GSOP	0.02 ± 0.05	0.29 ± 0.87		5 ± 3
G x GC	0.08 ± 0.01	0.54 ± 0.17	0.05 ± 0.03	4 ± 1
G x GW	0.02 ± 0.01	0.21 ± 0.17	0.15 ± 0.06	0
NSOP	0.09 ± 0.09	0.47 ± 0.37		1 ± 4
N x NC	0.05 ± 0.05	0.39 ± 0.32	0.00 ± 0.00	0

[a] Population GOP = *E. globulus* open-pollinated progeny from trees in native stands,

GSOP = *E. globulus* open-pollinated progeny from trees in seed orchards,

G x GC = Intra-provenance full-sib *E. globulus* crosses ("close" crosses),

G x GW = Inter-provenance full-sib *E. globulus* crosses ("wide" crosses),

NSOP = *E. nitens* open-pollinated progeny from trees in seed orchards, and

N x NC = Intra-provenance full-sib *E. nitens* crosses

[b] For the GOP, the estimate of σ^2_{fe} was zero, thus $r_{Bg} = 1$. The variance of the σ^2_{fe} estimate and the estimates of covariance between σ^2_{fe} and other variance components in the model are set to zero by SAS VARCOMP REML. Using these values, the standard error of the r_{Bg} estimate would be also be zero, but this is not particularly meaningful

with the dbh of 4-year-old *E. nitens* ($h^2 = 0.21$, very little G x E).

Coefficient of relationship for seed orchard families

Estimates of outcrossing in seed orchards are higher than in native stands, and results of the present study indicate moderately low amounts of inbreeding depression in the NSOP and GSOP populations. Therefore, it might be more appropriate to consider seed orchard open-pollinated families as very nearly true half-sib families. If so, an $r = 0.25$ is appropriate, and this would have the impact of doubling all heritability estimates for the GSOP and NSOP populations in Tables 3 and 4 (r_{Bg} estimates would not be affected). When heritabilities are calculated for the GSOP and NSOP populations using $r = 0.25$, the estimates are still substantially higher than the corresponding full-sib estimates in both the single-site (Table 3) and cross-site analyses (Table 4), specifically, 2- and 3.5-times for the *E. globulus* and *E. nitens* populations, respectively. This result would suggest that, in fact, seed orchard open-pollinated families are *not* true half-sib families, and may contain enough full-sibs (as well as progenies from selfing and other forms of related matings) to increase the coefficient of relationship. Flowering has been shown to be highly heritable in these seed orchards, and asynchronous flowering exists between provenances (Volker et al. 1988). Thus it is possible that a particular tree in a seed orchard could be pollinated by only a very few males which could contribute to this result.

Predicted breeding values

Parental breeding values were predicted using data from each population across all sites. In other words, each *E. globulus* parent had three predicted breeding values: one based only on the GOP male or the GSOP female, one based only on G x GC data, and one based only on G x GW data. Each *E. nitens* parent had two breeding-value predictions: from the NSOP and N × NC data. According to genetic theory, the correlation between the predicted breeding value and the unknown true breeding value [i.e., Corr$(g,\hat{g})$] can be calculated for given amounts of data, assuming known genetic parameters (White and Hodge 1989). A value of Corr $(g,\hat{g}) = 1$ would indicate a prediction with zero error; as Corr $(g,\hat{g})$ approaches zero, the error variance associated with the breeding-value predictions increases. In this study, the average estimated Corr $(g,\hat{g})$ was 0.69 for the NSOP breeding-value predictions, 0.93 for the GOP predictions, and was approximately 0.80 for the other four populations. A value of Corr $(g,\hat{g}) = 0.93$ for the GOP indicates that we have a precise measure of the genetic superiority or inferiority exhibited by the progeny of a particular tree when it is used as a parent of a native stand open-pollinated family. A Corr $(g, \hat{g}) = 0.80$ for the G × GW population indicates that we have a precise measure of the average genetic superiority or inferiority exhibited by the progeny of a particular tree when it is used as a parent in inter-provenance full-sib crosses. Since these measures (which in this manuscript are both called "breeding values") are from populations with different genetic structures, they do not necessarily measure the same genetic effects. To assess this, correlations among the breeding values from the different populations were examined.

For *E. globulus*, the only significant correlation between the parental breeding-value prediction developed from the different populations was between the G × GC and G × GW populations ($r = 0.54$, $P = 0.001$, see Table 5). The breeding-value predictions from the GOP population had near-zero correlations with those from the G × GC and G × GW populations. The correlations between the GSOP breeding-value predictions and the G × GC and G × GW predictions were negative, although they were non-significant. For *E. nitens*, the correlation between the predictions from the NSOP and the N × NC populations was 0.61, which is significant at $P = 0.08$ based on only nine parents.

Table 5 Correlation between parental breeding value predictions for 2-year-old volume made from data from different progeny populations for *E. globulus* and *E. nitens*[a]

Corr(BV_i,BV_j) *P*-value no. of parents	G × GC	G × GW	N × NC
GOP	0.21 0.31 25	0.13 0.51 25	
GSOP	−0.46 0.29 7	−0.11 0.79 8	
G × GC		0.54 0.001 33	
NOP			0.61 0.08 9

[a] Population GOP = *E. globulus* open-pollinated progeny from trees in native stands,
GSOP = *E. globulus* open-pollinated progeny from trees in seed orchards,
G × GC = Intra-provenance full-sib *E. globulus* crosses ("close" crosses),
G × GW = Inter-provenance full-sib *E. globulus* crosses ("wide" crosses),
NSOP = *E. nitens* open-pollinated progeny from trees in seed orchards, and
N × NC = Intra-provenance full-sib *E. nitens* crosses

Griffin and Cotterill (1988) assert that, despite various confounding factors, native stand open-pollinated progeny test results may still have utility in tree improvement programs. They suggest that good growth in an OP test indicates a high breeding value (in CP tests), but poor OP performance does not necessarily indicate a poor breeding value in CP tests. This held reasonably true in the present study when selecting on the basis of the GOP breeding value for the G × GC breeding value. Despite the correlation of 0.21 between the GOP and G × GC breeding values (Table 5), seven of the top eight GOP parents were above average in G × GC breeding value (ranks 4, 6, 7, 8, 10, 12, 13, and 24 with 25 parents in common), while only five of the bottom eight GOP parents were below average (ranks 3, 9, 11, 14, 16, 17, 22, and 23). Selection on the basis of GOP breeding value for the G × GW breeding value was not particularly good at identifying either good or poor performers. The top eight GOP parents contained equal numbers of above and below average performers (ranks 5, 8, 9, 10, 15, 17, 19, and 22), while only five of the bottom eight GOP parents were below average for G × GW breeding value (ranks 3, 6, 11, 14, 16, 20, 21, 23). This reflects the lower correlation between GOP and G × GW (0.13, Table 5), perhaps due to intra-provenance versus inter-provenance performance differences although the correlation between G × GC and G × GW breeding values was reasonably high ($r = 0.54$).

For *E. nitens*, the NSOP rankings appear to be quite useful in selection for the N × NC breeding value. Not only is the correlation between the predictions reasonably high (0.61, Table 5), but the top three parents for NOP breeding value are ranked identically for the N × NC breeding value. In contrast, the GSOP breeding values have no utility in selection, and actually have a slight negative (non-significant) correlation with both the G × GW and G × GC breeding values. This may possibly be due to the large dominance variance apparently present in inter-provenance crosses of *E. globulus*, combined with non-random mating in the orchard. Estimates of $h^2 = 0.02$ and $r_{Bg} \approx 0.25$ for the GSOP and G × GW populations are nearly identical (Table 4); thus, it seems reasonable that the estimate of $d^2 = 0.15$ for the G × GW population applies to the GSOP. If only a few near-neighbors act as male parents for a given GSOP family, the large effects due to dominance may completely confound the small effects due to additive effects. The same hypothetical situation in *E. nitens* would be much less of a problem due to larger heritabilities and zero dominance (Table 4). If dominance is causing some "noise" in the relationship between GSOP breeding values and G × GW breeding values, this situation may change with age as there is evidence in some coniferous tree species that, relative to additive variance, dominance variance decreases with age (Balocchi et al. 1993).

General discussion

There are some striking similarities between the results of this study for *E. globulus* and those of Griffin and Cotterill (1988) and Hardner and Potts (1995 b) for *E. regnans*, the only other authors to compare genetic parameter estimates from OP and CP populations. The most interesting result is the inflation of h^2 estimates derived from native stand open-pollinated progeny collected from native stands. Borrahlo (1994) has shown by modelling that heritability estimates from open-pollinated progenies will be inflated by increasing heterogeneity of selfing rates and inbreeding depression. This inflation was considered small compared to that induced by assigning the wrong genetic correlation between open-pollinated sibs. However, the only empirical comparisons of open-pollinated progenies from native stands of *Eucalyptus* (e.g., present study, Griffin and Cotterill 1988; Hardner and Potts 1995 b) have shown that heritabilities for early growth are inflated beyond that predicted by models (e.g., Squillace 1974; Borrahlo 1994). This inflation does not appear to be due to incorrect assumptions regarding the proper coefficient of relationship (r) for native stand open-pollinated families (*r* assumed equal to 0.40 and 0.50 in the two studies). The empirical evidence suggests that there are other factors to consider such as the frequency of full-sibs, large dominance effects, and the impact of relatively major deleterious gene effects.

Native stand open-pollinated families grew significantly slower than full-sib outcross families (17% reduction for *E. globulus* and 12% for *E. regnans*), which is very likely attributable to inbreeding depression from selfing and related matings. Within-plot variance (σ_w^2) was inflated in all OP populations in this study, possibly indicating some selfing. Similarly, Hardner and Potts (1995 a) found variance inflation in self and OP families of *E. globulus* compared to polymix outcross families. However, increases in σ_w^2 for open-pollinated progeny were not observed by Griffin and Cotterill (1988) for *E. regnans*. Griffin and Cotterill did find large differences among *E. regnans* parents in both inbreeding depression, resulting from selfing, and in the rate of outcrossing. Differences in self sterility in *E. globulus* have also been observed (Potts and Savva 1988). As a result, inherent growth differences among native stand open-pollinated families could be confounded with large differences among parents for these two traits. Clearly, correlations between parental breeding-value predictions based on observed growth performances of open-pollinated families and control-pollinated families would then be reduced.

Differential inbreeding depression among native stand open-pollinated families from native stands could also cause an underestimate of genotype × environment interaction and an overestimate of r_{Bg}. It seems reasonable that inbreeding depression would be a relatively "hard" type of genetic effect, i.e., independent of environment; thus differences among families in out-crossing and inbreeding depression would tend to be consistently observed site after site.

The value of native stand open-pollinated tests for selection in *E. nitens* may be higher than for *E. globulus*. Comparing GSOP to NSOP, the NSOP population suffers less inbreeding depression, and comparing G × GC to N × NC, the N × NC population has no dominance variance (Table 4). *E. nitens* also has less deleterious abnormalities at the seedling stage than *E. globulus* (Potts et al. 1992; Potts and Jordan 1994). Perhaps native stand open-pollinated populations of *E. nitens* would also exhibit minimal inbreeding depression, and problems arising from pollination by few males would not be exacerbated by additional "noise" from dominance variance.

Progeny of tests using open-pollinated seed from native stands are quite common in *Eucalyptus* species (Eldridge et al. 1993). For example, a collection of 600 open-pollinated seed lots collected from native stands of *E. globulus* are currently being tested at numerous sites in Portugal, Chile, Spain, China and Australia. (Eldridge et al. 1993; Potts and Jordan 1994). The results of this study suggest that breeders should be cautious about intensive family selection on the basis of these kinds of tests. While the tests may be helpful in indicating families and/or offspring selections to use in production populations for commercial reforestation, eliminating large numbers of families from the breeding population would probably result in the loss of many potentially valuable genotypes.

Conclusions

Several conclusions can be drawn from this study although they should probably be regarded as tentative due to the young age of the test material. Heritability estimates for early growth of open-pollinated progenies derived from native stands of *Eucalyptus* may be severely inflated, even if relatively high coefficients of relationship are assumed. The primary cause appears to be inbreeding depression from selfing and/or related matings. Differential frequencies of selfing and/or related mating, combined with a differential depression response to inbreeding, would inflate native stand open-pollinated family differences, and thus inflate heritability estimates. Additional contributing factors could include few effective males and large dominance effects. It appears to be appropriate to assume a high coefficient of relationship in seed orchard open-pollinated families also, perhaps due to a small number of effective males for any given open-pollinated family. The severity of these effects appear to depend on the genetic architecture of the species. The present study suggests that *E. nitens* has lower levels of non-additive genetic variation, lower levels of deleterious abnormalities (also see Potts et al. 1992), and displays less inbreeding depression compared to *E. globulus*, so that the prediction of parental breeding values from open-pollinated progeny from native stands is more comparable to the breeding values predicted from control-cross full-sib progeny.

Higher levels of dominance variance were observed in intra-provenance crosses than in presumably more closely related inter-provenance crosses in *E. globulus*. There are indications that parents of superior native stand open-pollinated families also tend to be above average in control-pollinated tests. On the other hand, culling families from the breeding population on the basis of poor performance in native stand open-pollinated tests will most likely risk the loss of good genetic material.

Genetic gains from open-pollinated populations may have been overestimated due to (1) inflation of heritability estimates through the use of OP data (Tables 2–4), (2) failure to account for site × genotype interaction (Table 2), (3) poor correlation between OP performance and true breeding value, presumably measured without bias in CP tests (Table 5). Site × genotype interaction may have been underestimated due to the inclusion of inbreeding effects in the comparisons among families across sites.

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