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EFFECTS OF INBREEDING ON GROWTH AND WOOD PROPERTIES OF SELFED *EUCALYPTUS UROPHYLLA* PROGENIES

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WU SJ, XU JM, LU ZH, LI GY, PAN LQ & HAN C. 2015. Effects of inbreeding on growth and wood properties of selfed *Eucalyptus urophylla* progenies. Growth, wood properties and bark percentage were assessed in 4-year-old inbred progenies of *Eucalyptus urophylla* in southern China. Analysis of variance showed significant site effects for all traits except for bark thickness and stress wave velocity. There were significant differences in diameter at breast height over bark, basic density, stress wave velocity and modulus of elasticity at the 0.01 level between replicates and significant differences in studied traits at the 0.01 level between combinations. Inbreeding depression of growth traits were found in U21, U22, U56 and DU1 progenies at Du-hui, U2, U21, U56, U64 and DU1 at Gong-he and U56 at Feng-an. U56 had the largest inbreeding depression ranging from -17.73 to -80.89% in three sites. For basic density and dynamic modulus of elasticity, the improvement found for U56 both at Du-hui and Gong-he implied that U56 could be used to improve *E. urophylla* wood properties by inbreeding. Generally, the same parents at different sites showed different levels of inbreeding depression. Different traits had different inbreeding depressions even on the same parent at the same site. Important implications for breeding strategy are that inbreeding can be effective in improving *E. urophylla* and selfed progeny may prove useful for estimation of genetic parameters and future breeding.

Keywords: Inbred progenies, crossbreeding, multiple traits, breeding strategy

INTRODUCTION

Systematic forestry breeding plan began in China in the 1950s and the poplar breeding plan was developed from 1950s till 1960s (Chen 2001, Xu 2003). Successful improvement of *Eucalyptus* focusing on wood volume was achieved. However, companies involved in large-scale productions of *Eucalyptus* need other factors to be included that can reduce specific wood consumption or industrial processing cost such as wood basic density, bark percentage and modulus of elasticity (Wu et al. 2004, Bison et al. 2007). To develop sound breeding strategies, it is necessary to understand both the reproductive biology and breeding system of a species (Horsley & Johnson 2007).

Compared with other *Eucalyptus* species growing in China, *E. urophylla* is a very important plantation species in tropical and subtropical areas (Chen et al. 2006, Lu 2009, He et al. 2012). It was introduced into southern China in the 1980s under the Australia–China Programme of Technical Cooperation (McKenney 1998). *Eucalyptus urophylla* is native to some islands of Indonesia and East Timor and represents one of the best low-latitude eucalypts for planting in tropical areas, within latitudinal range from 7° S to 10° S and altitudinal range of 90 to 3000 m (FAO 1979, Wright & Osorio 1996, Xu et al. 2001, Qi 2002, Kien et al. 2009, He et al. 2012). Just like Brazil and Congo, superior clones for cellulose production have been developed mainly through interspecific hybridisation (natural or controlled pollination) between *E. urophylla* and *E. grandis* and other species. Good performance for wood volume was observed in hybrid combinations in China (Hardy et al. 2002, Bueren 2004, Bison et al. 2007, Luo et al. 2010, Wu et al. 2013).

Inbreeding can reduce the number of new combinations of genotypes on which future genetic gain by selection depends, whether

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from seed orchards or plantations (Butcher & Williams 2002). Therefore, inbreeding has been recognised as an important research tool for forest genetics and breeding because it can impact the heredity structure, substantially increase reproductive ability as well as seed quality and quantity (Chen et al. 1989). Inbreeding may become an effective breeding method in some species. Inbreeding has been reported on *E. camaldulensis* (Butcher & Williams 2002), *E. urophylla* (Horsley & Johnson 2007), *E. grandis* (Horsley & Johnson 2007), *E. nitens* (Hardner & Tibbits 1998), *Pinus radiata* (Matheson et al. 2002, Wu et al. 2004), *Acacia mangium* (Harwood et al. 2004) and *Populus nigra* (Benetka et al. 2008). Butcher and Williams (2002) reported that the high mean outcrossing rates for four populations of *E. camaldulensis*, together with low proportion of variation in growth attributed to outcrossing rate, suggested that inbreeding was unlikely to be a problem in the first generation of tree improvement using open-pollinated families sourced from natural populations in the Petford region. However, Chen et al. (1989) reported that the germination rate and growth traits of fir sharply decreased after multiple-generation inbreeding and inbreeding depression was enhanced as the inbreeding generation increased. Compared with outcrossing, the germination rate of inbred, backcrossed, full-sib and half-sib combinations decreased by 88, 42, 20 and 20% respectively while the height of progenies decreased by 27, 17, 13 and 13% respectively (Chen et al. 1989).

Inbreeding is a fertilisation system which involves the crossing of individuals that are closely related (Benetka et al. 2008) and is well known to result in depression of growth in many forest tree genera and species (Woods et al. 2002, Harwood et al. 2004). Strong inbreeding depression has been observed at different life stages in many forest trees, including fecundity (Wu et al. 2004), seed development (Chen et al. 1989, Horsley & Johnson 2007), growth performance in nurseries (Woods et al. 2002), and during the early stage of field trials (Griffin & Cotterill 1988, Hardner & Tibbits 1998, Butcher & Williams 2002, Matheson et al. 2002, Harwood et al. 2004, Bison et al. 2006, Benetka et al. 2008). Pollen tubes from self-pollination were reported to take longer time than those from cross-pollination to reach the base of the style in both *E. urophylla* and *E. grandis* and both species exhibited reduced seed yields following self-pollination compared with cross-pollination (Horsley & Johnson 2007). However, inbreeding depression may not be expressed to the same degree across all traits (Hardner & Tibbits 1998). The most common estimates of inbreeding depression involve traits that are closely related to growth, seed development and fitness in several *Eucalyptus* species. However, inbreeding reports on growth traits and wood properties in *E. urophylla* at one or more sites are limited.

In this paper, we examine the level of inbreeding depression of *E. urophylla* 4 years after planting. This trial provided estimates of inbreeding depression for later growth traits and wood properties at three sites. The information is important for development of breeding strategies for this species.

MATERIALS AND METHODS

Site

The trials were established at Du-hui, Gong-he and Feng-an in Guangdong province in April 2006. The locations and descriptions of sites and details of soil of the three progeny trials are presented in Tables 1 and 2. The field design was randomised complete block with six replications and 5-tree line plots planted with spacing of 3 m × 2 m. Planting pits (50 cm × 50 cm × 40 cm) were prepared and compound fertiliser was applied in the first 2 years with individual tree applications. The dominant plants in the undergrowth of the original tree canopy included *Dicranopteris pedata, Mussaenda pubeseens* and *Rhodomyrtus tomentosa.*

Material

The full-diallel mating design was made from August till October 2004. The details of parents and combinations are listed in Table 3. Seeds were collected in April 2005 at Duhui. All full-diallel combinations and open pollination progenies of six parents were used in the trial. However, the value of inbreeding combinations and open pollination progenies were only analysed to estimate inbreeding depression.

Table 1 Location and description of field sites

Location	Xinhui Duhui	Heshan Gonghe	Zijin Fengan
Latitude	22° 33' N	22° 34' N	23° 25' N
Longitude	113° 03' E	112° 51' E	114° 50' E
Altitude (m)	45	30	100
Rainfall (mm year^{-1})	1750	1750	1752
Soil	Lateritic red earth	Lateritic red earth	Lateritic red earth
Mean annual temperature (°C)	22.3	22.3	20
Absolute minimum temperature (°C)	16.7	16.7	16–17
Absolute maximum temperature (°C)	28.3	28.3	26–27
Spacing (m)	3 × 2	3 × 2	3 × 2
Number of blocks	6	6	6

Table 2 Nutrient content of soil at three sites

Site	pH	Organic content (g kg^{-1})	Total N (g kg^{-1})	Total P (g kg^{-1})	Total K (g kg^{-1})	Available N (mg kg^{-1})	Available P (mg kg^{-1})	Available K (mg kg^{-1})	Available B (µg g^{-1})
Du-hui	4.51	29.979	1.218	0.417	11.523	99.30	0.99	52.06	0.26
Gong-he	4.10	12.790	0.422	0.175	5.129	34.25	0.53	21.63	0.26
Feng-an	4.64	8.391	0.319	0.172	1.064	22.91	5.98	15.28	0.17

Table 3 Full-diallel mating design among six *Eucalyptus urophylla* parents

Female parent	Male parent					
	U2	U21	U22	U56	U64	DU1
U2	☐	×	×	×	×	×
U21	×*	☐	×	×	×	×
U22	×	×	☐	×	×	×
U56	×	×	×	☐	×	×
U64	×	×*	×	×	☐	×
DU1	×	×	×	×	×	☐

× cross combination, ☐ inbreeding combination, ×* seeds of this combination were not collected

Data collection

Measurements and 5-mm diameter increment cores were made in April 2010 when the trial was 4 years old. Diameter at breast height over bark (DBHOB in cm) and height (HGT in m) were measured for all trees. All progenies were assessed for Pilodyn penetration (PP) and stress wave velocity (SWV) using Pilodyn and Fakopp microsecond timer tools respectively.

Individual tree volume over bark (VOL in m^3) was calculated using the following formula as per McKenney et al. (1991):

$$\mathrm{VOL} = \mathrm{HGT} \times \mathrm{DBHOB}^2 / 30{,}000 \qquad (1)$$

Bark percentage (Bark %) for each tree was defined as the ratio of the area of bark at breast height (1.3 m) to total cross-sectional area at the same height (Wu et al. 2011).

$$\text{Bark \%} = \frac{\mathrm{DBHOB}^2 - (\mathrm{DBHOB} - 2\mathrm{BT})^2}{\mathrm{DBHOB}^2} \times 100\% \qquad (2)$$

where BT (cm) = average bark thickness measured by callipers.

Wood basic density (BD) was determined using the water displacement method, with two weights for every sample: weight of water displaced by immersion of core (w_1) and oven dry weight (w_2) (Kien et al. 2008, Wu et al. 2010, Wu et al. 2011). It was calculated as:

$$\mathrm{BD}\ (\mathrm{g\ cm^{-3}}) = w_2 / w_1 \qquad (3)$$

PP was measured using Pilodyn fitted with 2.5 mm steel pin by removing a small section of the bark (40 mm × 20 mm) at 1.3 m and making two Pilodyn shots in this bark window. PP was recorded on two of the four directions (north, south, east and west) for a randomly selected tree within each plot without visible disease symptoms.

The Fakopp microsecond timer is a tool that records SWV (Wu et al. 2011). The stress wave transmission time (i.e. time of flight) was measured three times. SWV was calculated by dividing the test span by the mean stress wave transmission time (Wang et al. 2000) in km $\mathrm{s^{-1}}$.

$$\mathrm{SWV} = L / t \qquad (4)$$

where
L = 1500 mm = distance between start and stop probes
t = transmission time (μs).

The SWV may be used as indicator of stiffness in itself or combined with density measurements to give an estimate of dynamic modulus of elasticity (MOE) (Wang et al. 2000).

$$\mathrm{MOE} = \rho\omega^2 \qquad (5)$$

where MOE = modulus of elasticity, ρ = green wood density of the stem (g $\mathrm{cm^{-3}}$), ω = SWV (m $\mathrm{s^{-1}}$).

Statistical analysis

Statistic analyses were conducted using GLM procedures in SAS statistical software to detect differences between sites, replications and combinations for growth traits and wood properties as well as bark percentage. The line model on one trait, y_{ijk} is

$$y_{ijk} = \mu + E_i + B_{j(i)} + C_k + \varepsilon_{ijk} \qquad (6)$$

where Y_{ijk} = phenotypic value of the individual of the kth combination in jth block within ith site, μ = overall mean, E_i = fixed effect of ith site, $B_{j(i)}$ = fixed effect of jth block within ith site, C_k = fixed effect of kth combination and ε_{ijk} = random error (or residual).

Inbreeding depression (D_i) was estimated as

$$D_I = \frac{F_{si} - \overline{OP}}{\overline{OP}} \times 100\% \qquad (7)$$

where F_{si} = average value of studied traits for the inbred progenies of parents, $\overline{OP}$ average value of studied traits for open pollination progenies of parents (Jin et al. 2009).

RESULTS AND DISCUSSION

Variance between clones and replicates

The analyses of variance of studied traits between replications and combinations at different sites are presented in Table 4. Site effects reflect the reaction of trees to the combined effects of edaphic as well as local and regional climatic conditions (Pliura et al. 2006). The joint analysis of all three trials showed significant site effects for all traits except for BK and SWV. Site effects were much smaller for BK and SWV, as evidenced by lower F values, indicating that trees had less phenotypic plasticity for these characters. There were significant differences in DBHOB, BD, PP and SWV at the 0.01 level between replicates at different sites at least in part due to the relatively uneven site. The differences in HGT, VOL, BK, Bark % and MOE between replicates were not significant suggesting less environmental effects on these traits. There were significant differences in studied traits at the 0.01 level between combinations, with F values ranging from 0.97 to 10.22, indicating clear differences between combinations.

Analysis of inbreeding depression of growth traits and wood properties

The estimates of inbreeding depression for studied traits are listed in Table 5. Inbreeding depression of growth traits was observed in U21, U22, U56 and DU1 at Du-hui. U21 had the largest inbreeding depression estimated as

-26.34, -28.21 and -59.62% for HGT, DBHOB and VOL respectively. However, improvement of growth traits was found in inbred crosses of U2 and U64. Furthermore, growth traits and wood properties were all improved and BK, Bark % and PP displayed favourable decreases suggesting that inbred U2 could be used for *E. urophylla* improvement in China. Inbreeding depression of growth traits was also found in the studied parents except for U22 at Gong-he, while U56 also had the largest inbreeding depression with estimates of -17.73, -19.91 and -46.00% for height, DBHOB and volume respectively. These findings were in agreement with studies by Benetka et al. (2008) and Chen et al. (1989). Benetka et al. (2008) observed that traits of plant height, trunk diameter, height increment and resistance to *Melampsora larici-populina* were lower in comparison with those of open pollinated offspring. Wu et al. (2004) observed that despite significant inbreeding depression in the percentage of female reproductive trees and

Table 4 Analyses of variance of studied traits at three sites

Trait	Site		Replication		Combination	
	F value	Probability	F value	Probability	F value	Probability
Degree of freedom	2		5		39	
HGT	531.38	< 0.0001	2.18	0.0541	10.22	< 0.0001
DBHOB	182.36	< 0.0001	4.05	0.0012	8.06	< 0.0001
VOL	36.13	< 0.0001	0.78	0.5630	2.38	< 0.0001
BD	68.64	< 0.0001	2.79	0.0163	3.29	< 0.0001
BK	1.52	0.2196	1.48	0.1922	2.61	< 0.0001
Bark %	19.29	< 0.0001	0.60	0.7037	2.05	0.0002
PP	6.06	0.0024	3.86	0.0018	3.51	< 0.0001
SWV	1.65	0.1921	5.69	< 0.0001	3.06	< 0.0001
MOE	13.71	< 0.0001	0.17	0.9724	0.97	0.5195

HGT = height, DBHOB = diameter at breast height over bark, VOL = volume, BD = wood basic density, BK = bark thickness, Bark % = bark percentage, PP = Pilodyn pin penetration, SWV = stress wave velocity, MOE = dynamic modulus of elasticity

Table 5 Estimations of inbreeding depression for growth traits and wood properties in *Eucalyptus urophylla* at three sites (%)

Site	Parent	HGT	DBHOB	VOL	BD	BK	Bark %	PP	SWV	MOE
Du-hui	U2	5.15	2.71	2.53	6.61	-7.28	-10.18	-4.73	1.12	15.20
	U21	-26.34	-28.21	-59.62	-4.94	-32.39	-6.59	-7.69	-11.81	-21.91
	U22	-11.42	-11.53	-18.75	-2.52	-16.60	-5.38	-2.47	0.76	-9.93
	U56	-18.17	-20.30	-55.12	13.41	-5.68	12.43	-9.77	4.84	18.49
	U64	12.81	13.79	28.53	-8.05	-2.05	-13.10	5.25	0.50	-8.26
	DU1	-11.23	0.00	-24.97	-11.29	34.69	25.79	23.15	-1.19	-12.10
Gong-he	U2	-0.59	-6.57	-8.74	-1.58	-11.41	-5.30	-2.20	-0.32	-0.29
	U21	-16.60	-13.89	-34.09	-8.00	-19.58	-8.23	5.15	-6.09	-13.77
	U22	19.50	12.64	25.38	4.44	-23.80	-28.73	3.03	-0.23	–
	U56	-17.73	-19.91	-46.00	7.00	-11.63	10.77	-4.59	-2.73	2.07
Feng-an	U56	-43.74	-41.46	-80.89	–	-15.79	41.22	4.28	-5.51	–

HGT = height, DBHOB = diameter at breast height over bark, VOL = volume, BD = wood basic density, BK = bark thickness, Bark % = bark percentage, PP = Pilodyn pin penetration, SWV = stress wave velocity, MOE = dynamic modulus of elasticity; dash indicates value not available the number of cones on adult trees, the overall impact of inbreeding depression on fecundity was low in radiata pine. Griffin and Cotterill (1988) found that the volume of outcross progenies averaged 37% more than the selfs of *E. regnans*. U56 was the only parent planted at Feng-an and the estimates of inbreeding depression were -43.74, -41.46 and -80.89% for HGT, DBHOB and VOL respectively. Harwood et al. (2004) analysed self-fertilised individuals and observed that they were significantly slower growing than outcrossed individuals, with selfs on average 15% smaller in mean HGT and 16% smaller in mean DBHOB at age 18 months, relative to outcrossed plants.

The results of inbreeding depression for growth traits and wood properties in *E. urophylla* at the three sites showed that the same parents planted at different sites displayed different levels of inbreeding depression. Different traits revealed different levels of inbreeding depression even in the same parent at the same site, indicating that inbreeding could be used effectively to produce favourable improvement in a combination of traits. Hardner and Tibbits (1998) found that growth traits (HGT, DBHOB, basal area and VOL) and the number of flower buds exhibited significant inbreeding depression whereas inbreeding depression was absent for wood density, relative bark thickness, frost damage and the proportion of reproductively mature individuals in *E. nitens*. In terms of BD and MOE, inbreeding depression was not found in U2 and U56 at Du-hui as well as U22 and U56 at Gong-he, suggesting that U56 might be used to improve BD and MOE of *E. urophylla* by inbreeding. In general, the largest inbreeding depression was found in VOL of U56 at Feng-an and the greatest improvement was found in Bark % of U56 at Feng-an. This suggests that it is difficult to gain improvement of *E. urophylla* growth traits with inbred U56.

Joint analysis of all three trials in the present study suggested three implications for *E. urophylla* tree improvement in China. Primarily, the role of parent selection during the initial phase of inbreeding of *E. urophylla* requires re-examination. Secondly, inbreeding can be used effectively for *E. urophylla* improvement and selfed progeny may prove useful for estimation of genetic parameters and future breeding. Finally, inbreeding depression is not a static value for studied traits in different environments. The environmental factors affecting the offspring will therefore be important in determining what impact inbreeding depression will have on natural populations.

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