

GENETIC PARAMETERS IN FIBRE TRAITS FROM A FULL DIALLEL OF *EUCALYPTUS UROPHYLLA* IN SOUTHERN CHINA

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Fibre traits were assessed for 6 × 6 full-diallel families of *Eucalyptus urophylla* measured at 10 years old. Analysis of variance showed that there were significant combination effects and no block differences on any fibre traits except fibre width. The mean fibre length, fibre width, fine percent, mean curl, fibre kink index and kink angle of controlled crossed families were 0.57 mm, 19.74 µm, 27.38%, 0.039°, 0.64 and 8.24° respectively. The heritability of fibre traits was at low to middle level, and the coefficients of variation ranged from 8.58 (width) to 39.30% (kink angle). Inbreeding depressions of fibre length and width were observed in most families, and the largest inbreeding depressions were estimated at -61.76 and -15.45%. Heterosis ranged from -42.42 to 103.84%. Kink angle had higher general combining ability and fine percent had higher estimation of specific combining ability. Genotypic correlation between fibre length and fibre width were positive, implying these two traits could be selected simultaneously. As an important indicator of pulp yield, fibre traits should be used for breeding *E. urophylla*.

Keywords: Heterosis, breeding strategy, fibre length, fibre width, kink index

INTRODUCTION

After more than 30 years of testing and domestication, the genetic improvement in wood volume of *Eucalyptus* is remarkable. Unfortunately, the mean annual harvest in volume of eucalypt plantations in China is lower than that in the tropical and subtropical regions of the other parts of the world (Xu 2003, Toit et al. 2010). Thus, greater effort to improve productivity of eucalypt plantations in China should be put into practice.

The diallel mating system is an altered factorial design in which the same individuals (or lines) are used as both male and female parents (Huber et al. 1992). Diallel mating design is an important tool in tree breeding because it can provide breeders useful genetic information, such as general combining ability (GCA), specific combining ability (SCA) and heterosis to help them devise appropriate breeding and selection strategies (Yanchuk 1996, Xiang & Li 2001, Zhang et al. 2005). Extensive studies of diallel mating design have been reported for *Eucalyptus* species, such as for *E. grandis* (Wyk 1976), *E. globulus* (Bison et al. 2007, Rix et al. 2012), *E. nitens* (Volker et al. 2008) and *E. urophylla* (Bison et al. 2007, Retief & Stanger 2009, Wu et al.

2015). Li et al. (2002) reported that growth traits and stem properties of *E. globulus* are controlled by GCA, SCA and specific reverse cross effects. Heterosis, or hybrid vigour, is a phenomenon in which F₁ hybrids perform better than their parents in terms of biomass, yield or resistance to environmental challenges (Dapp et al. 2015). Heterosis is a quicker, cheaper and easier method of increasing plant production (Kalhor et al. 2015). Genetic improvement of wood properties affecting the quality of pulpwood products is of general interest to tree breeders worldwide (Blackburn et al. 2012). Fibre traits are essential for pulpwood and paper quality and include fibre length, fibre width, fine percent, mean curl, kink index and kink angle. The fibre with higher length, greater width and higher fine percent has higher intensity while the fibre with higher mean curl, kink index and kink angle has higher water absorption.

Eucalyptus urophylla is naturally distributed on mountain slopes and valleys of the large island of Timor and the nearby Indonesian islands of Wetar, Alor, Pantar, Lomblen, Adonara and Flores (Wright & Osorio 1996, Kien et al. 2008). *Eucalyptus urophylla* was introduced into southern

China in the 1980s under the Australia–China Program of Technical Cooperation (McKenney 1998). It has since become a very important plantation species in tropical and subtropical areas in China (Chen et al. 2006, He et al. 2012). More than 50% of widely used clones in China were established with germplasm derived from *E. urophylla* and interspecific hybridisation with *E. urophylla* via controlled pollination (Luo et al. 2010, Wu et al. 2013, Chen et al. 2018). Comprehensive research results about provenance trials, family tests and clone selection of *E. urophylla* were published in recent years (Retief & Stanger 2009, Andrade et al. 2013). Unfortunately, full diallel analysis, especially estimation of GCA, SCA and heterosis have not been used very much in *E. urophylla* improvement.

In this paper, we compared the variance of different combinations, estimated the coefficients of variation of different fibre traits, examined the GCA and SCA and investigated heterosis value of different crosses from 6 × 6 full diallel *E. urophylla* trials at 10 years old. This information will be used to develop appropriate breeding strategies for this species in southern China.

MATERIALS AND METHODS

Plant materials and trait measurement

The trials were established at Du-hui (22° 33' N, 113° 03' E, 45 m asl) in Jiangmen city of Guangdong Province in April 2006. Maximum rainfall occurs during summer, while winters are generally dry and cool. The mean rainfall per year is 1750 mm. The soil is classified as lateritic red earth. Organic content, pH, total N, total P, total K and average B are 29.98 g kg⁻¹,

4.51, 1.22 g kg⁻¹, 0.42 g kg⁻¹, 11.52 g kg⁻¹ and 0.26 g kg⁻¹ respectively. The field design was a randomised complete block with six replications and five-tree line plots planted at spacing 3.0 m × 2.0 m. Planting pits (50 cm × 50 cm × 40 cm) were prepared and compound fertiliser was applied in the first two years with individual tree applications. The 6 × 6 full-diallel mating design was made in August to October 2004. Thirty-four full diallel combinations and open pollination families of six parents were collected in April 2005 (Table 1) and used in this trial.

Increment cores (5-mm diameter) were collected from two of five trees in one plot and 12 samples were collected from each family in the trial. Cores were macerated using a sodium hydroxide and peracetic acid digestion (Kube et al. 2001, Wu et al. 2011). Fibre traits including fibre length, fibre width, fine percent, mean curl, kink index and kink angle were measured on 10,000 randomly selected fibres from each core using a fibre analyser.

Statistical analysis

Statistical analyses were conducted using ASreml package in R statistic software to detect difference of variance. The linear model on one trait, y_{ijkl} , is:

$$y_{ijkl} = \mu + B_i + F_j + M_k + S_{jk} + R_{jk} + P_{ijk} + e_{ijkl} \quad (1)$$

where μ = general mean, B_i = fixed effect of replicate i , F_j and M_k = GCA of female j and male k (random effect), S_{jk} = SCA of parents j and k (random effect), R_{jk} = random effect of the specific cross (reciprocal effect) between female j and male k , P_{ijk} = random effect of individual and e_{ijkl} = random residuals (Fukatsu et al. 2013). Narrow sense heritability (h^2) derived from both male and female parents was estimated as:

Table 1 Full-diallel mating design between six *Eucalyptus urophylla* parents

| Female | Male | | | | | |
|--------|----------------|----------------|-----|-----|-----|-----|
| | U2 | U21 | U22 | U56 | U64 | DU1 |
| U2 | ⊙ | × | × | × | × | × |
| U21 | × [#] | ⊙ | × | × | × | × |
| U22 | × | × | ⊙ | × | × | × |
| U56 | × | × | × | ⊙ | × | × |
| U64 | × | × [#] | × | × | ⊙ | × |
| DU1 | × | × | × | × | × | ⊙ |

× = cross combination, ⊙ = inbreeding combination, # = combination seeds were not obtained

$$h^2 = 2(\sigma_f^2 + \sigma_m^2) / (\sigma_f^2 + \sigma_m^2 + \sigma_{fm}^2 + \sigma_e^2) \quad (2)$$

where σ_f^2 , σ_m^2 , σ_{fm}^2 and σ_e^2 are female effect, male effect, female and male interaction effect and error effect respectively.

The genotypic coefficient of variation (CV) was calculated as (Pliura et al. 2007, Hai et al. 2008):

$$CV = (100\sigma_c / \bar{x}) \times 100\% \quad (3)$$

where σ_c = genetic variance and \bar{x} = phenotypic mean. The equation expresses a standardised measure of the genetic variance relative to the mean of trait. Inbreeding depression (D_i) was estimated following Jin et al. (2009):

$$D_i = (F_{si} - OP) / OP \times 100\% \quad (4)$$

where F_{si} = average value of studied traits for inbred families of parents and OP = average value of studied traits for open pollination families of parents.

F_1 hybrid heterosis was calculated as follows (Bahman et al. 1975):

$$H = (F_i - OP) / OP \times 100\% \quad (5)$$

where F_i = average value of studied traits for hybrid families, OP = average value of studied traits for open pollination families of better parent. The genotypic correlation, $r_{A(xy)}$, of traits x and y was calculated as (Pliura et al. 2007, Stackpole et al. 2010):

$$r_{A(xy)} = \frac{\sigma_{a(xy)}}{\sqrt{\sigma_{a(x)}^2 \times \sigma_{a(y)}^2}} \quad (6)$$

where $\sigma_{a(x)}^2$ = genetic variance components for the trait x , $\sigma_{a(y)}^2$ = genetic variance components for the trait y and $\sigma_{a(xy)}^2$ = additive covariance component.

RESULTS

Variance among families and blocks

The analyses of variance of studied fibre traits among blocks, family, male and female are listed in Table 2. The results showed that there were no significant block differences in all fibre traits except fibre width and no significant block \times family difference for all fibre traits, indicating that fibre width was affected by environment. The joint analysis of all families showed significant family effects for all fibre traits except fibre width. This suggested that there was less difference in fibre width between combinations. Furthermore, there were significant differences in fibre width, mean curl, kink index and kink angle among females and significant differences in fibre width and mean curl among males, and fine percent and mean curl between female \times male effect.

Trait mean, heritability and genetic variation

Mean value, heritability and coefficient variation of the studied fibre traits are presented in Table 3. Open-pollinated families had longer mean fibre length than controlled crossed families, whereas the mean values of fibre width, fine percent, mean curl, kink index and kink angle of the latter were greater than the former. Heritability of studied fibre traits had middle to low value (0.2 is middle, > 0.4 is high). Fibre width had

Table 2 Variance analysis for fibre traits of *Eucalyptus urophylla*

| Trait | Block | | Progeny | | Block \times progeny | | Female | | Male | | Female \times male | |
|--------------|-------|--------|---------|--------|------------------------|--------|--------|----------|------|--------|----------------------|--------|
| | F | P | F | P | F | P | F | P | F | P | F | P |
| Fibre length | 0.55 | 0.8134 | 1.64 | 0.0226 | 1.02 | 0.4626 | 1.70 | 0.1352 | 1.96 | 0.0862 | 1.57 | 0.0537 |
| Fibre width | 3.87 | 0.0005 | 1.39 | 0.0936 | 0.61 | 0.9966 | 2.55 | 0.0288 | 3.99 | 0.0018 | 0.88 | 0.6316 |
| Fine percent | 1.21 | 0.2949 | 2.09 | 0.0013 | 1.06 | 0.3790 | 1.58 | 0.1661 | 1.16 | 0.3292 | 2.38 | 0.0007 |
| Mean curl | 1.38 | 0.2131 | 1.86 | 0.0059 | 0.68 | 0.9848 | 6.03 | < 0.0001 | 2.38 | 0.0400 | 1.62 | 0.0409 |
| Kink index | 1.66 | 0.1147 | 1.99 | 0.0025 | 0.78 | 0.9160 | 6.92 | < 0.0001 | 1.81 | 0.1115 | 1.57 | 0.0536 |
| Kink angle | 1.66 | 0.1151 | 1.83 | 0.0072 | 0.73 | 0.9589 | 6.87 | < 0.0001 | 1.16 | 0.3278 | 1.55 | 0.0568 |

F = F-ratio, P = the probability of the F-ratio

the highest heritability estimation than other traits, and fine percent had the lowest heritability estimation. The coefficient of variation of fibre ranged from 8.58 to 39.30%. Kink index had the highest estimation value compared with the rest of the traits, and fibre width had the lowest estimation.

Inbreeding depression analysis

The estimates of inbreeding depression for studied fibre traits are listed in Table 4. Inbreeding depression of fibre length was observed in parents U2, U21, U56, U64 and DU1 while U64 had the largest inbreeding depression. Inbreeding depression of fibre width was observed in parents U21, U56 and U64 while U64 had the largest inbreeding depression. The depression of fine percent, mean curl, kink index and kink angle ranged from -67.16 to 205.20%. DU1 had positive inbreeding depression value of fibre width and negative inbreeding depression value of the rest of the traits.

Heterosis estimation

Estimations of heterosis on fibre traits in *E. urophylla* families are given in Table 5. For positive heterosis, fibre length, fibre width, fine percent, mean curl, kink index and kink angle were

estimated at -30.63 to 4.44%, -9.20 to 10.74%, -22.25 to 62.36%, -19.21 to 51.79%, -28.04 to 54.27 and -25.64 to 94.62% respectively. U56 × DU1 had the highest positive heterosis estimation on kink angle while U2 × U64 had the lowest positive heterosis estimation on fibre length. On the other hand, the reverse heterosis estimation on fibre length, fibre width, fine percent, mean curl, kink index and kink angle were -26.47 to 16.35%, -8.68 to 9.07%, -42.42 to 75.55%, -18.48 to 70.50%, -31.68 to 61.78 and -31.22 to 103.84% respectively. U56 × U21 had the highest reverse heterosis estimation on kink angle, while U64 × U2 had the lowest reverse heterosis estimation on fine percent.

Estimation of GCA and SCA

The estimation of GCA and top 10 SCA of fibre traits between crosses are listed in Tables 6 and 7. The results showed that kink angle had higher GCA estimation, and fine percent had smaller GCA estimation (Table 6). Different parents had similar GCA estimation of fine percent. DU1 had higher GCA estimation on fibre length and fibre width and lower GCA estimation on mean curl, kink index and kink angle. Fine percent had higher SCA estimation and mean curl had smaller GCA estimation (Table 7). SCA estimation for fibre length was relatively higher

Table 3 Mean values for traits, heritability (h^2) and coefficient of variation (CV) of *Eucalyptus urophylla* fibre

| Type | Fibre length (mm) | Fibre width (μm) | Fine percent | Mean curl ($^\circ$) | Kink index | Kink angle ($^\circ$) |
|-----------------------------|-------------------|-------------------------------|--------------|------------------------|------------|-------------------------|
| Controlled crossed families | 0.57 | 19.74 | 27.38 | 0.039 | 0.64 | 8.24 |
| Open-pollinated families | 0.59 | 19.61 | 27.15 | 0.037 | 0.61 | 7.83 |
| h^2 | 0.08(0.09) | 0.19(0.13) | 0.01(0.06) | 0.14(0.13) | 0.18(0.15) | 0.14(0.12) |
| CV (%) | 19.90 | 8.58 | 8.98 | 27.50 | 39.30 | 39.01 |

Table 4 Inbreeding depression of fibre traits (%) of *Eucalyptus urophylla*

| Parent | Fibre length | Fibre width | Fine percent | Mean curl | Kink index | Kink angle |
|--------|--------------|-------------|--------------|-----------|------------|------------|
| U2 | -21.34 | 6.22 | 53.53 | 38.89 | 89.70 | 77.30 |
| U21 | -38.04 | -9.52 | 113.43 | 122.22 | 205.20 | 193.52 |
| U22 | 37.81 | 11.11 | -61.28 | 7.14 | 12.16 | 15.47 |
| U56 | -9.44 | -5.82 | -20.53 | 47.50 | 54.23 | 50.78 |
| U64 | -61.76 | -15.45 | 190.01 | 57.14 | 61.40 | 54.74 |
| DU1 | -1.32 | 8.42 | -16.79 | -40.00 | -67.16 | -67.32 |

Table 5 Heterosis on fibre traits of *Eucalyptus urophylla*

| Combination | Positive heterosis % | | | | | Reverse heterosis % | | | | | | | |
|-------------|----------------------|-------------|--------------|-----------|------------|---------------------|-------------|--------------|-------------|--------------|-----------|------------|------------|
| | Fibre length | Fibre width | Fine percent | Mean curl | Kink index | Kink angle | Combination | Fibre length | Fibre width | Fine percent | Mean curl | Kink index | Kink angle |
| U2 × U21 | -6.22 | 0.06 | 7.83 | 11.69 | 27.07 | 23.97 | U21 × U2 | / | / | / | / | / | / |
| U2 × U22 | 4.17 | -9.20 | -4.21 | -7.81 | -5.47 | -8.47 | U22 × U2 | -21.44 | -3.29 | 28.82 | 70.50 | 61.78 | 59.47 |
| U2 × U56 | 4.44 | -6.07 | -22.25 | -19.21 | -21.99 | -25.64 | U56 × U2 | -25.57 | -8.68 | 75.55 | 46.86 | 18.58 | 48.30 |
| U2 × U64 | -30.63 | -5.87 | 62.36 | 23.17 | 23.57 | 18.32 | U64 × U2 | 16.35 | -3.37 | -42.42 | -9.89 | -10.31 | -13.18 |
| U2 × DU1 | 3.18 | 4.65 | -11.97 | -14.10 | -28.04 | -30.01 | DU1 × U2 | -9.26 | 8.01 | 15.30 | -7.88 | -22.25 | -23.92 |
| U21 × U22 | -8.48 | 4.27 | 39.75 | 21.39 | 30.06 | 34.25 | U22 × U21 | -2.80 | -4.90 | -22.11 | -0.10 | 0.30 | -1.59 |
| U21 × U56 | -4.01 | 2.66 | 34.82 | 40.50 | 54.27 | 61.09 | U56 × U21 | 0.27 | -3.08 | 18.41 | 41.63 | 57.58 | 103.84 |
| U21 × U64 | -10.34 | 6.20 | 35.25 | 28.18 | 37.53 | 37.40 | U64 × U21 | / | / | / | / | / | / |
| U21 × DU1 | -8.88 | 10.74 | 36.23 | 25.04 | 15.52 | 19.81 | DU1 × U21 | 8.71 | 9.07 | 7.90 | -16.58 | -24.95 | -31.22 |
| U22 × U56 | -9.11 | -1.85 | -17.53 | 21.88 | 27.27 | 22.83 | U56 × U22 | 13.85 | -3.89 | 12.82 | 9.05 | 6.02 | 41.77 |
| U22 × U64 | -2.48 | 5.38 | -10.67 | 3.00 | 1.49 | -3.63 | U64 × U22 | 9.08 | -1.88 | -20.61 | -13.99 | -9.94 | -17.72 |
| U22 × DU1 | -7.19 | 0.50 | 4.90 | 12.50 | 21.26 | 20.21 | DU1 × U22 | 0.04 | 7.30 | -18.83 | -18.48 | -31.68 | -30.21 |
| U56 × U64 | -0.81 | -2.43 | -11.30 | 10.86 | 5.34 | 33.53 | U64 × U56 | -26.47 | -6.44 | 23.37 | 19.05 | 25.80 | 9.30 |
| U56 × DU1 | -0.63 | 8.44 | 30.94 | 51.79 | 41.36 | 94.62 | DU1 × U56 | -8.77 | 8.50 | 16.14 | -17.46 | -26.60 | -28.91 |

Positive heterosis = heterosis estimation of combinations in the above diagonal of Table 1, reverse heterosis = heterosis estimation of combinations in the below diagonal of Table 1

Table 6 General combining ability for fibre traits of *Eucalyptus urophylla*

| Parent | Fibre length | Fibre width | Fine percent | Mean curl | Kink index | Kink angle |
|--------|----------------|----------------|---------------|----------------|----------------|----------------|
| U2 | 0.0043 (0.02) | -0.0683 (0.25) | 0.0000 (0.00) | 0.0018 (0.00) | 0.0615 (0.06) | 0.8599 (0.62) |
| U21 | 0.0014 (0.02) | -0.2224 (0.25) | 0.0000 (0.00) | 0.0007 (0.00) | 0.0299 (0.05) | 0.4064 (0.60) |
| U22 | 0.0128 (0.02) | -0.2946 (0.24) | 0.0000 (0.00) | -0.0014 (0.00) | -0.0287 (0.05) | -0.3060 (0.59) |
| U56 | -0.0194 (0.02) | -0.0674 (0.25) | 0.0000 (0.00) | 0.0040 (0.00) | 0.0871 (0.05) | 0.7753 (0.62) |
| U64 | -0.0134 (0.02) | 0.3368 0.22 | 0.0000 (0.00) | -0.0021 (0.00) | -0.0882 (0.05) | -1.0420 0.61) |
| DU1 | 0.0144 (0.02) | 0.3159 (0.24) | 0.0000 (0.00) | -0.0030 (0.00) | -0.6147 (0.05) | -0.6936 (0.60) |

Standard errors are given in parentheses

Table 7 Specific combining ability for fibre traits of *Eucalyptus urophylla*

| Fibre length | Combination | Fibre width | Combination | Fine percent | Combination | Mean curl | Combination | Kink index | Combination | Kink angle | Combination |
|--------------|-------------|-------------|-------------|--------------|-------------|-----------|-------------|------------|-------------|------------|-------------|
| 0.028 | U64 × U2 | 0.335 | U56 × DU1 | 9.506 | U64 × U56 | 0.007 | U22 × U2 | 0.099 | U56 × U56 | 1.057 | U56 × U56 |
| 0.027 | DU1 × U64 | 0.241 | DU1 × U21 | 5.893 | U56 × U2 | 0.004 | U56 × DU1 | 0.074 | U22 × U2 | 0.950 | U2 × U21 |
| 0.023 | DU1 × U21 | 0.235 | U64 × U22 | 5.277 | U64 | 0.003 | U56 × U56 | 0.072 | U2 × U21 | 0.947 | U22 × U2 |
| 0.017 | U22 | 0.159 | U64 | 4.811 | U21 × U21 | 0.003 | U2 × U64 | 0.071 | DU1 | 0.933 | DU1 |
| 0.016 | U21 | 0.140 | DU1 × U64 | 3.841 | U2 × U22 | 0.003 | U21 × U21 | 0.058 | U56 × U21 | 0.808 | U56 × U21 |
| 0.015 | U21 × U56 | 0.117 | U22 × U22 | 3.782 | U2 × U64 | 0.003 | U2 × U21 | 0.048 | U2 × U64 | 0.673 | U21 × U56 |
| 0.014 | U2 × U22 | 0.112 | U2 × DU1 | 3.313 | U64 × U64 | 0.002 | U64 × U56 | 0.044 | U21 × U56 | 0.641 | U56 × DU1 |
| 0.013 | U56 × U2 | 0.106 | DU1 × U56 | 2.265 | DU1 × U2 | 0.002 | U56 × U2 | 0.029 | U64 × U56 | 0.597 | U2 × U64 |
| 0.012 | U22 × U21 | 0.106 | U22 × U64 | 2.080 | DU1 × U56 | 0.002 | U64 × DU1 | 0.028 | U64 × DU1 | 0.400 | U22 × DU1 |
| 0.010 | U2 × U56 | 0.105 | U2 × U2 | 1.952 | U56 × DU1 | 0.002 | DU1 | 0.027 | U56 × DU1 | 0.378 | U64 × DU1 |

Estimates of specific combining ability are given for the top 10 values

in U22 and U21 open-pollinated combinations than the rest of the parents while U64 had higher SCA estimation for fibre width. SCA estimation was highest in U64 × U56, U22 × U2, U56 × U56 and U56 × U56 for fine percent, mean curl, kink index and kink angle respectively.

Trait–trait genetic correlation

Genotypic correlation between fibre traits is listed in Table 8. In this study, fibre length had positive genotypic correlation with fibre width and fine percent, ranging from 0.06 to 0.38. However, both fibre length and fibre width had negative correlation values with mean curl, kink index and kink angle, ranging from -0.36 to -0.99. Generally, there were strong positive genotypic correlation values between fine percent, mean curl, kink index and kink angle, ranging from 0.27 to 1.00.

DISCUSSION

Means and genetic parameters of traits

Higher fibre length could improve the quality of paper. In the study, the present mean fibre length values of all the families (Table 3) are shorter than the widely used eucalypt hybrid clones (Yao et al. 2003, Wu et al. 2011), indicating that more attention should be paid to fibre length in the breeding of pure *E. urophylla*. Meanwhile fibre width is higher than values reported for *E. tereticornis* and *E. camaldulensis* families (Lu et al. 2000). The 8-year-old *E. tereticornis* and *E. camaldulensis* in Hainan Province, south China had mean values for fibre length ranging from 0.83 to 1.16 mm and fibre width from 11 to 13 µm (Lu et al. 2000).

Estimates of heritability for fibre traits were low to medium for fibre percent (0.01) and fibre width (0.19), which were in general agreement with the eucalypt hybrids studied by Zhu et al. (2017) (0.04) and Chen et al. (2018) (0.06–0.49). Heritability of fibre width was higher than that of fibre length, indicating more genetic gain could be obtained from fibre width by genetic improvement as previously found by Wu et al. (2011).

The coefficient of variation of fibre traits in this study ranged from 8.58% for fibre width to 39.30% for kink angle (Table 3). The coefficient of variation of fibre width was in general agreement with the variability observed by Wu et al. (2011). However, the coefficient of variation of fibre length was larger than published papers, implying that the selection gain would be limited.

Inbreeding is useful for improvement

Inbreeding has been recognised as an important research tool for forest genetics and breeding because it impacts the heredity structure and substantially increases reproductive ability as well as seed quality and quantity (Chen et al. 1989). However, improvement in fibre length and fibre width was observed in inbred crosses of parent U22 suggesting that inbred parent U22 could be used for *E. urophylla* improvement in China. Generally speaking, different parents had different inbreeding depression on different fibre traits. It was interesting to find that there was no inbreeding depression on mean curl, kink index and kink angle in inbreeding of parents U2, U21, U22, U56 and U64. This meant that their inbred offspring could improve water absorption of paper.

Table 8 Genotypic correlations between fibre traits of *Eucalyptus urophylla*

| Trait | Fibre width | Fine percent | Mean curl | Kink index | Kink angle |
|--------------|-------------|---------------|--------------|--------------|--------------|
| Fibre length | 0.34 (0.45) | 0.38 (0.30) | -0.79 (0.51) | -0.36 (0.32) | -0.66 (0.48) |
| Fibre width | | (0.06) (0.15) | -0.99 (1.57) | -0.80 (0.31) | -0.89 (0.33) |
| Fine percent | | | 0.79 (0.53) | 0.67 (1.48) | 0.48 (1.37) |
| Mean curl | | | | 1.00 (0.13) | 0.27 (1.05) |
| Kink index | | | | | 1.00 (0.01) |

Standard errors are given in parentheses

Different combinations had different positive and reverse heterosis

Heterosis values were estimated as the percentage deviation of the F_1 performance from the midparent, better parent and best parent (Paramathma et al. 1997). In general, the estimation range of reverse heterosis was greater than that of positive heterosis (Table 5). The positive and reverse heterosis estimation ranges for fibre length were greater than that for fibre width. The same combinations had different positive and reverse heterosis even for the same traits. For example, the positive and reverse heterosis for fibre length of U2 and U22 were 4.17 and -21.44% respectively. Meanwhile U2 × DU1 and DU1 × U21 had higher positive and reverse heterosis for fibre length and fibre width. This implied that superior individuals with higher fibre length and width can be selected from these combinations. Bao and Luo (2002) reported that heterosis estimation for growth and wood traits ranged from -9.4 to 23.2% in 9-year-old *E. urophylla*.

GCA and SCA analysis

Combining ability provides a guideline for selecting elite parents and desirable cross combinations to be used in formulation of a systematic breeding project for rapid improvement (Kalhor et al. 2015). For fibre length and width, U56 had negative GCA effect while DU1 had positive effect (Table 6), indicating DU1 had higher general combining ability and potential to improve fibre length and width simultaneously. It is interesting to find that the GCA effect of kink index may have slight positive correlation with GCA effect of kink angle. For fibre length, U64 × U2, DU1 × U64 and DU1 × U21 had higher SCA estimation while U56 × DU1, DU1 × U21 and U64 × U22 had higher SCA estimation for fibre width (Table 7). This showed that these families could be used for further propagation and breeding.

Genetic correlation between traits

High genetic correlation value between growth traits and wood properties had been widely described in *Eucalyptus* and other species (Kien et al. 2009, Kube et al. 2001, Wu et al. 2011, Chen et al. 2018). High genetic correlation indicates

that the expression of both traits is most likely controlled by the same class of genes in an organism (Chen et al. 2018). There was positive genotypic correlation between fibre length, fibre width and fine percent, meaning that longer fibre length always had higher fibre width and higher fine percent. Meanwhile positive genotypic correlation values were observed between fine percent, mean curl, kink index and kink angle. However negative genotypic correlation was observed between fibre length and width and mean curl, kink index and kink angle, indicating that higher fibre length and width always had lower mean curl, kink index and kink angle. Our results were consistent with previous studies that reported strong positive correlation between fibre length and fibre width for *Eucalyptus* hybrid clones in southern China (Wu et al. 2011).

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