ORIGINAL ARTICLE

Sapling and coppice biomass heritabilities and potential gains from *Eucalyptus polybractea* progeny trials

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Abstract

Eucalyptus polybractea has been planted as a short-rotation coppice crop for bioenergy in Western Australia. Historical breeding selections were based on sapling biomass and despite a long history as a coppice crop, the genetic parameters of coppicing are unknown. Here, we assessed sapling biomass at ages 3 and 6 from three progeny trials across southern Australia. After the second sapling assessment, all trees were harvested. Coppice biomass was assessed 3.5 years later. Mortality following harvest was between 1 and 2%. Additive genetic variance for the 6-sapling estimate at one site was not significant. Sapling heritabilities were between 0.06 and 0.36 at 3 years, and 0.18 and 0.20 at 6 years. The heritability for the coppice biomass was between 0.07 and 0.17. Within-site genetic and phenotypic correlations were strong between all biomass assessments. Cross-site correlations were not different from unity. Selections based on net breeding values revealed positive gains in sapling and coppice biomass. Lower or negative gains were estimated if 3-year sapling selections were applied to the coppice assessments (−7.1% to 3.4%) with useful families culled. Positive gains were obtained if 6-year sapling selections were applied to the coppice assessment (6.4% to 9.3%) but these were lower than those obtained by applying coppice selections to the coppice assessment (8.4% to 14.8%). Removal of poor performing families and families that displayed fast sapling growth rates but under-performed as coppice will benefit potential coppice production. These results indicate that selections should be made using coppice data.

Keywords Coppice biomass · *Eucalyptus polybractea* · Net breeding values · Heritability · Sapling biomass · Genetic and phenotypic correlations · Selection simulation

Introduction

A suite of mallee *Eucalyptus* sp. were selected for short-rotation coppice crops in Western Australia (WA) for essential oils, bioenergy and biofuel feedstocks (Bartle and Abadi 2010; Davis 2002; McGrath et al. 2016). Species selections were based on the ability to coppice vigorously after harvest with high concentration of foliar 1,8-cineole (Hobbs et al. 2009). One of the successful candidates for development was *Eucalyptus polybractea* R.T. Baker which has been harvested on a 2-year cycle in Victoria and New South Wales (NSW) for high-grade eucalyptus oil production for over a century (Davis 2002; Goodger et al. 2007). Agroforestry trials in WA have demonstrated that *E. polybractea* is capable of high productivity when grown on sites with acidic deep soil profiles with low salinity (Spencer et al. 2019; Wildy et al. 2000). In 1993 an *E. polybractea* breeding programme was initiated with three small progeny trials (Bartle et al. 1998). Additional trials were added in later years and included progeny from 100 families using seed from wild parents with cineole concentrations of >2.5% (Mazanec et al. in press).

In order to maximise the potential of *E. polybractea* for cineole production, breeding focused on gains in foliar 1,8-cineole concentration for the high-grade eucalyptus oil market (Boland et al. 1991; Coppen 2002; Davis 2002). The market for eucalyptus oil with high levels of 1,8-cineole did not materialise and the potential for biomass for bioenergy (Abdullah and Wu 2009; McGrath et al. 2016; Wu et al. 2008) emerged as a greater potential avenue for profit (Bartle and Abadi

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2010). Breeding decisions for *E. polybractea* on biomass performance have historically been based on assessment of sapling performance although the relationship between sapling and coppice biomass is unknown. Studies in other eucalypt species have revealed a wide range of genetic correlations between sapling and coppice biomass ranging from weak (Whittock et al. 2003) to very strong (Amâncio et al. 2020; Li et al. 2012). This variation in genetic correlations may be underpinned by the genetic control of lignotuber development, which has been found to be responsible for the varying degrees of success of coppicing (Bortoloto et al. 2020; Walters et al. 2005; Whittock et al. 2003).

The mallee species developed as coppice crops in WA, in contrast, show very high rates of reshooting after harvest (Eastham et al. 1993; Milthorpe et al. 1998; Spencer et al. 2019) suggesting that lignotuber development in these species is less variable. For example, resprouting from the lignotubers, *E. kochii*, does not appear to be limited by either the number of meristematic foci or starch reserves, but rather a loss of fine root material and reduction of thickening of structural rootstock following too frequent harvesting (Wildy and Pate 2002). Subsequent work across four trial-plantings has demonstrated that for *E. polybractea*, a rotation length of 3 years is appropriate for sustainable biomass production (Spencer et al. 2019). However, greater gains in biomass production may be realised if a breeding programme is focused on coppice productivity following harvest.

The heritability of desirable traits underpins the accuracy of selection of elite individuals or families for genetic gain. If multiple traits are of interest, it is of critical importance to understand the genetic relationships between them, as selection for one trait may result in correlated gains or losses in another (Isik et al. 2017). For instance, Milthorpe et al. (1998) observed that selection of individuals based on foliar eucalyptus oil concentration alone may reduce total oil production, and for two subspecies of *E. loxophleba*, weak negative correlations have been observed between biomass and foliar cineole concentrations (Mazanec et al. 2020; Mazanec et al. 2017). Currently, there are no published estimates of genetic parameters for *E. polybractea* pertaining to coppice biomass. Knowledge of the genetic correlations between sapling and coppice biomass production at different ages as well as between subsequent coppice cycles is essential for determining the optimal time for selection for biomass production.

Eliminating inferior genotypes will improve both biomass and 1,8-cineole yields and will assist in the economic viability of any future *E. polybractea* industry.

This paper reports the results of a study investigating (1) the heritability of coppicing success and biomass production, (2) the correlations between sapling and coppice biomass across three progeny trials established across southern Australia and (3) the optimal timing of selection through simulations of trial thinning for conversion to seed orchards and establishment of clonal orchards.

Methods

Study sites

Three progeny trials were planted in 2009 at the Condobolin Agricultural Research Station in NSW (33.07° S, 147.24° E), Drummartin in Victoria (36.44° S, 114.43° E) and at the Newdegate Research Station in WA (33.12° S, 118.82° E). All sites have mild winters and hot summers with Drummartin and Newdegate receiving most of their rainfall in the winter months while rainfall at Condobolin is more evenly distributed throughout the year (Table 1). Climate and elevation data were sourced from the Australian Bureau of Meteorology stations located at the Condobolin and Newdegate Research Stations and Drummartin town site. The soil at Newdegate is duplex with yellow sand over clay, Drummartin is a duplex with grey-brown loam over sodic red clay while at Condobolin, the soil is gradational red and brown earths (Mazanec et al. in press).

Each of the three progeny trials consisted of the same 66 open-pollinated families. All parent trees were randomly selected from native stands in the region of West Wyalong in NSW. The trials were planted in a Latinised row-column design with families randomly assigned to four-tree row plots. There were six replicates at Condobolin and Drummartin. However, space constraints at the Newdegate trial required a configuration with four replicates and five-tree row plots. Planting spacing of 1.5 m was applied within each row, and rows were 3 m apart. Each trial had a two-tree buffer surrounding the entire trial using the same species with unknown progeny.

In the spring of 2016, each trial, including buffer trees, was cut as close to ground level as possible using chainsaws.

Table 1 Average climatic conditions during the trial period (2009 to 2020) at the three progeny trial locations. Climatic and elevation data were obtained from Bureau of Meteorology (SILO 2020)

Trial location	Annual rainfall (mm)	Annual evaporation (mm)	Maximum temperature (°C)	Minimum temperature (°C)	Elevation (m)
Condobolin	491	2245	27.8	11.9	195
Drummartin	471	1720	25.2	10.0	115
Newdegate	359	1904	26.3	9.6	320

Biomass assessments

Each trial was measured twice before harvest, once when the trials were in their third year (spring 2012 to autumn 2013) and again in spring 2016 when the saplings were about 6 years. Coppice post-harvest was measured in autumn 2020. For the initial sapling and coppice assessments, the height and crown widths (in two perpendicular directions) of each mallee were measured to the closed 5 cm using a surveyor's staff. The Crown Volume Index (CVI) was calculated as the product of those three measurements as described in Spencer et al. (2019). At the initial measurement at Drummartin, both stem basal area (SBA) and CVI were measured. The SBA method was used in the second assessment (2016) where the stems of each mallee were measured at 10 cm above ground level with a diameter tape. Where there were multiple stems, each diameter was converted cross-sectional stem areas and was summed to give the total cross-sectional stem areas as described by Huxtable et al. (2012).

After the 3-year sapling measurement, between 46 and 53 buffer trees, representative of the size of the trial trees, were measured and then destructively sampled. After the second biomass assessment, an additional 40 trees were destructively sampled from each trial. Linear regressions relating SBA or CVI to above-ground biomass were used to estimate above-ground tree biomass. The regression parameters for the initial assessment are detailed in Mazanec et al. (in press). For the coppice assessment, species-specific *E. polybractea* coppice biomass allometric equations were used to estimate above-ground green biomass (Spencer et al. 2019).

Data analysis

Allometric equations between SBA and biomass were developed using SAS Proc Reg on natural log transformed data (SAS 2017). The equations took the form:

$$\ln(y) = \ln(a) + b \ln(x) + \varepsilon \tag{1}$$

where y is the above-ground green biomass, x is the SBA, a is the intercept, b is the slope and ε denotes the model residuals. To remove bias inherent to back-transforming from logarithmic to original scale, the Baskerville (1972) correction was applied.

Analysis of heritability and genetic parameters was conducted using ASReml 4.1 (Gilmour et al. 2015) using the following linear mixed model:

$$Y = Xb + Zu + e \tag{2}$$

where Y is the phenotypic vector of observation, X is the fixed effects design matrix, b is the vector of fixed effects, Z is the random effects design matrix, u is the vector of the random effects and e is the vector residual error. Terms in b included the intercept and population effects while u included replicate, long column, row within replicate, column within replicate, plot and family effects.

Within the framework of the linear mixed model, we conducted three classes of analysis, as detailed in the following sections.

Univariate family model analyses

Univariate analyses, for each trial, were conducted to determine requirements for transformation prior to estimation of the fixed and random effects symbolised in b and u of Eq. 2. Terms in b included the intercept and population effects and terms in u included replicate, long column, row within replicate, column within replicate, plot and family effects. Residual plots were examined for heteroscedasticity. Mean-variance relationships and potential transformations were assessed using the slope of the log(absolute residual) on log(predicted value) as outlined by Gilmour et al. (2015). All biomass data required transformation. The 3-year sapling biomass was transformed to $x^{0.3}$ where x = 3-year-old sampling biomass (Mazanec et al. in press), the 6-year-old sapling biomass was subjected to $y^{0.0}$ where y = 6-year-old sapling biomass while coppice biomass was transformed using $z^{0.25}$ where z = coppice biomass. Univariate genetic parameters of the presences/absence of coppice post-harvest were analysed using the logit link function in ASReml with the same model specifications.

Univariate individual tree model

Once appropriate transformations were determined and applied, a univariate individual tree model was used to estimate additive genetic variances for biomass from each trial. Cases with significant additive genetic variance provided initial estimates of heritability and served as checks for subsequent analysis. Griffin and Cotterill (1988) observed that mixed mating systems in open-pollinated eucalypts may result in inflated heritability estimates. They suggested the use of a coefficient of relationship of $\rho = 1/2.5$ when estimating heritability to adjust for selfing rates of about 30%. Bush et al. (2011) affirmed that this methodology was applicable in first-generation open-pollinated eucalypts. Recently, Kainer et al. (2018) used the above coefficient of relationship when estimating heritability in *E. polybractea*. In our analysis, we also applied a selfing rate of 30% in ASReml to appropriately adjust additive variance estimate. Terms in u and b were the same between the family and individual tree models with the exception that the family term was replace by an individual tree random additive effect. The additive genetic variance between relatives was modelled via the numerator relationship matrix (Henderson 1976). The significance of individual variance

components was checked using a one-tailed log likelihood ratio test with 0.5 degrees for freedom (Gilmour et al. 2015).

Bivariate analyses

For this model, measurements of trees in different years were treated as different traits for the purpose of estimating genetic correlations. Terms in *b* and in *u* were the same as the univariate individual tree model, nested within trait. Estimated variances and covariances were used to calculate genetic correlations between the various biomass assessments. The genetic correlations were checked for significant deviation from zero and unity. To test for significant difference from zero, the correlation was constrained to zero and a two-tailed log likelihood ratio test with 1 degree of freedom was used. To test for significant difference from unity, the correlation was constrained to one and a one-tailed log-likelihood ratio test with 0.5 degrees of freedom was used.

Univariate cross-site analyses

For this model, terms in *b* included intercept and the site effects while terms in *u* were identical to the univariate individual tree model nested within site. Design effects and site variances were assumed independent between sites and genetic variances were assumed heterogenous. This model was used to estimate reported narrow-sense heritability for each site and cross-site genetic correlation. Cross-site genetic correlations were estimated on a pairwise basis and then checked for significant variation from zero and unity as described above.

An expanded version of the cross-site model was used to include family effects and site by family interaction effects as fixed terms in *b*. Design elements in *u* were as described above. This model was used to generate best linear unbiased estimates (BLUEs) for populations and families.

Narrow-sense heritability was estimated using the following formula:

$$\widehat{h}^2 = \frac{\sigma_a^2}{\left(\sigma_a^2 + \sigma_p^2 + \sigma_e^2\right)} \tag{3}$$

where $\widehat{h}^2$ is the narrow-sense heritability, σ_a^2 is the additive variance, σ_p^2 is the plot variance and σ_e^2 is the error variance.

Genetic and phenotypic correlations were calculated using the following formula:

$$r = \frac{\sigma_{12}^2}{\sqrt{\sigma_1^2 * \sigma_2^2}} \tag{4}$$

where r represents either the genetic correlation (r_g) or the phenotypic correlation coefficient (r_p) and σ_{12}^2, σ_1^2 and σ_2^2

represent either the additive genetic covariance and additive genetic variances or phenotypic correlation and phenotypic variances, respectively.

Net breeding values

Simulations of thinning trials for conversion to seed orchards were compared between years and between sapling and coppice on the basis of biomass. In order to evaluate the effect of selection at different sapling ages and between sapling and coppice, net breeding values (NBVs) for the three biomass assessments were estimated for each individual tree at each trial. For each assessment, a selection scheme using the NBV was applied to each trial for each sapling and coppice measurement, which simulated thinning the trials for conversion to seed orchards. In this process, the single individual with the highest NBV in a family plot was selected for retention if its NBV was above the mean NBV for the trial under consideration. If no trees in a plot satisfied that criterion, then no trees were retained in that plot. An additional selection scenario was performed to simulate selection for a clone orchard which included very high selection intensities of the best ten unrelated individuals at each trial.

For individual sites, NBV included the intercept, site, population and additive effects. Selection was conducted on the back-transformed scale and genetic gains were calculated using the percentage difference between the back-transformed mean NBV of the selected trees and of mean NBV of the trial.

To observe the impact on genetic gain of selection at the sapling stage, gain was recalculated using NBVs for coppice on the 3- and 6-year saplings' assessment and compared to the gain estimated when selecting for only coppice. Estimated genetic gains apply to redeployment of seedlings on the same site at which selections were made (Mazanec et al. in press).

Preliminary analysis indicated that additive variance for the 6-year sapling estimates at Drummartin was not significant ($P > 0.05$); therefore, heritabilities, genetic correlations and NBVs pertaining to that year were not estimated.

Results

Estimation of biomass

The allometric relationship (Eq. 1) between stem basal area and above-ground fresh biomass for the 6-year saplings was highly significant for each trial ($P < 0.0001$) (Table 2). Equations for 3-year sapling assessment are detailed in Mazanec et al. (in press), and for coppice biomass estimates, the species-specific E. polybractea equation was used from Spencer et al. (2019).

Table 2 Statistics of the site-specific allometric models that were used to estimate above-ground fresh biomass from stem basal area at the three progeny trials. Biomass ranges of sample trees included in the models are also shown. MSE is mean square error and R^2 is the coefficient of determination

Location	Biomass range (kg)	Slope	Intercept	MSE	R^2
Newdegate	0.2–119.1	1.195	−1.709	0.025	0.969
Drummartin	2.4–126.5	1.124	−1.415	0.032	0.974
Condobolin	0.5–84.0	1.105	−1.182	0.048	0.966

Trial biomass estimates

The back-transformed mean tree biomass at each of the three biomass assessments is given in Table 3. Growth rates were highest at the first assessment at Condobolin with a significant location effect ($P < 0.001$) and slowest growth at the Newdegate trial, but there appeared to be reversal of growth rates so that no significant differences were evident at the second measurement. Significant differences emerged again ($P < 0.001$) following the coppice assessment with faster growth rates at the Drummartin trial while rates at the other two sites were similar.

Mortality post-harvest

Post-harvest survival was very high across the three trials, ranging from 97.9% at Condobolin to 99.5% at Newdegate (Table 4). Across the 66 families, this ranged from 100% survival for 36 families to 94% for the worst performing family (Table S1). Due to the very high survival at each trial and the resulting insignificant additive variance for coppicing ability, heritability of survival post-harvest could not be estimated for each trial.

The untransformed phenotypic mean weight of the 6-year sapling estimates at Newdegate, Drummartin and Condobolin was 31.5, 28.2 and 28.7 kg while the corresponding phenotypic means for saplings that failed to coppice were 10.7, 15.3 and 11.4 kg at each trial, respectively.

Table 3 Back-transformed best linear unbiased estimates (BLUEs) of average tree biomass (kg) across the three *E. polybractea* progeny trials at each biomass assessment

Location	3-year sapling	6-year sapling	Coppice
Newdegate	5.2	26.5	11.8
Drummartin	8.5	22.9	26.0
Condobolin	11.5	24.5	11.0

Table 4 The number of saplings and coppice at each trial and the proportion that coppiced after harvest

Location	No. of saplings	No. of coppice	% coppiced
Newdegate	1117	1111	99.5
Drummartin	1290	1281	99.3
Condobolin	1362	1334	97.9

Effect of population on biomass performance

Ranking of biomass performances of the populations was highly variable with significant population effects across the three assessments ($P < 0.001$); however, the population by site interaction was not significant ($P > 0.05$) at each of the three assessments. Removal of three populations that were confounded with family (single family population) did not change the significance of any factor. For the 3-year sapling estimates, populations from West Yalgogrin, Tallimba Rd West and Charcoal Tank Road performed strongly ranking within the top 3 populations at two of the three trials (Table 5). In the second assessment, West Yalgogrin, Tallimba Rd West, Tallimba Rd East and Winters Lane all ranked in the top three at two of the three trials. Across both sapling assessments, West Mid-West Highway, West Wyalong Town and Kerrs Lane performed poorly, with Kerrs Lane performing last at five of the six assessments.

In assessment of biomass performances for the coppice, Charcoal Tank Road ranked in the top three at all three trials, Tallimba Road East at two trials. West Wyalong Town and Kerrs Lane were poor performers with Kerrs Lane ranking last at two trials. When the single parent trees were removed, Winters Lane ranked in the top two at all three trials while West Yalgogrin ranked top two at Newdegate and Condobolin and West Mid-West Highway ranked second at Drummartin.

Effect of family on biomass performance

Consistent with the population rankings, there was substantial family variation across assessments exemplified by significant family effect ($P < 0.001$) across all three assessments. There was also a significant family by site interaction effect in the first sapling assessments ($P < 0.01$) but this became non-significant in the 6-year sapling and coppice assessments ($P > 0.05$). Removal for the three families confounded with populations did not change the significance of any factor. Further assessment of the performance of the individual families is detailed in selection section below and the family estimates are provided in Tables S2, S3 and S4.

Table 5 BLUEs of biomass for each population at the three progeny trials with standard errors

Location	Population	Parent trees	3-year sapling	6-year sapling	Coppice
Newdegate	Charcoal Tank Rd	1	1.686 ± 0.095	3.268 ± 0.164	1.869 ± 0.092
	Kerrs Lane	2	1.520 ± 0.072	3.214 ± 0.115	1.840 ± 0.074
	Tallimba Rd East	1	1.586 ± 0.089	3.323 ± 0.147	1.805 ± 0.086
	Tallimba Rd West	1	1.712 ± 0.089	3.582 ± 0.155	1.962 ± 0.089
	West Mid-West Hwy	4	1.598 ± 0.057	3.053 ± 0.079	1.759 ± 0.062
	West Yalgogrin	4	1.666 ± 0.058	3.305 ± 0.081	1.873 ± 0.063
	Winters Lane	24	1.652 ± 0.045	3.325 ± 0.047	1.866 ± 0.054
	West Wyalong Town	29	1.629 ± 0.044	3.262 ± 0.046	1.857 ± 0.054
Average			1.631 ± 0.069	3.279 ± 0.041	1.856 ± 0.053
Drummartin	Charcoal Tank Rd	1	1.934 ± 0.101	3.272 ± 0.158	2.313 ± 0.085
	Kerrs Lane	2	1.764 ± 0.071	2.962 ± 0.109	2.085 ± 0.065
	Tallimba Rd East	1	1.882 ± 0.098	3.109 ± 0.154	2.192 ± 0.083
	Tallimba Rd West	1	1.780 ± 0.100	3.042 ± 0.162	2.223 ± 0.086
	West Mid-West Hwy	4	1.849 ± 0.053	2.993 ± 0.081	2.246 ± 0.053
	West Yalgogrin	4	2.003 ± 0.055	3.282 ± 0.084	2.189 ± 0.054
	Winters Lane	24	1.945 ± 0.029	3.215 ± 0.042	2.306 ± 0.042
	West Wyalong Town	29	1.867 ± 0.028	3.076 ± 0.040	2.241 ± 0.041
Average			1.878 ± 0.067	3.133 ± 0.034	2.257 ± 0.040
Condobolin	Charcoal Tank Rd	1	1.959 ± 0.086	3.074 ± 0.123	1.835 ± 0.065
	Kerrs Lane	2	1.869 ± 0.063	3.052 ± 0.087	1.736 ± 0.052
	Tallimba Rd East	1	2.108 ± 0.086	3.297 ± 0.120	1.849 ± 0.065
	Tallimba Rd West	1	2.190 ± 0.094	3.292 ± 0.137	1.922 ± 0.071
	West Mid-West Hwy	4	2.067 ± 0.049	3.144 ± 0.062	1.815 ± 0.044
	West Yalgogrin	4	2.068 ± 0.049	3.282 ± 0.063	1.827 ± 0.044
	Winters Lane	24	2.087 ± 0.032	3.196 ± 0.031	1.827 ± 0.036
	West Wyalong Town	29	2.093 ± 0.031	3.204 ± 0.029	1.816 ± 0.036
Average			2.055 ± 0.061	3.198 ± 0.024	1.821 ± 0.035

Genetic parameters

Biomass heritabilities were highest at the Condobolin trial with h^2 of 0.32 ± 0.08 for the 3-year sapling assessment, reduced to 0.18 ± 0.05 for the 6-year sapling assessment and 0.17 ± 0.05 for the coppice (Table 6). At Newdegate, heritabilities were lower for all three biomass assessments with the additive variance for coppice only marginally significant (P = 0.0497). At Drummartin, heritability for coppice was 0.07 ± 0.04 but additive variance was only marginally significant (P = 0.0497) for the 3-year sapling assessment and not significant for the 6-year sapling measurement (P > 0.05).

Within-site genetic correlations were high and significant (P < 0.005) between biomass assessments at the Newdegate and Condobolin trials with low standard errors ranging from 0.65 ± 0.12 to 1.07 ± 0.17 (Table 6). These were significantly different from unity between all assessments at Condobolin and between the two sapling assessments at Newdegate (P < 0.05) but not significant between the coppice and sapling assessments (P > 0.05). At both trials, the lowest genetic correlations were between the 2016 sapling and the 2020 coppice estimate. Very high genetic correlations were estimated for the 3- and 6-year sapling estimate (2013 and 2016) and the first sapling and the coppice estimate (2013 and 2020). At Drummartin, a weak genetic correlation was estimated for the 3-year sapling and coppice assessments (r_g = 0.47 ± 0.31) due to the weak additive variance and was significantly different from unity (P < 0.01).

In contrast to the genetic correlations, phenotypic correlations were lowest between the 3-year sapling measurement and the coppice measurement which ranged from r_p = 0.67 ± 0.02 to 0.73 ± 0.02 (Table 6). The strengths of the correlations were stronger between the two sapling measurements (r_p = 0.79 ± 0.01 to 0.88 ± 0.01). The phenotypic correlations were stronger between coppice and 6-year saplings (r_p = 0.75 ± 0.01 to 0.80 ± 0.01) than between coppice and 3-year saplings (r_p = 0.67 ± 0.02 to 0.73 ± 0.02).

Cross-site genetic correlations were very high between Newdegate and Condobolin (0.82 ± 0.15 to 0.94 ± 0.13) with low standard errors for both sapling estimates and were very high for the coppice estimate but with higher standard errors (0.93 ± 0.31) (Table 7). The 3-year sapling genetic correlation

Table 6 Heritabilities, genetic and phenotypic correlations ± standard errors for the 3- and 6-year sapling biomass assessments (2013 and 2016) and coppice assessment (2020) from the three mallee progeny trials. Heritabilities on the diagonal (in bold) with genetic and phenotypic correlations respectively above and below the diagonal entries. For cases with non-significant additive genetic variance, heritability and genetic correlations are denoted ns (non-significant)

	Newdegate			Drummartin			Condobolin		
	2013	2016	2020	2013	2016	2020	2013	2016	2020
2013	**0.20 ± 0.07**	0.84 ± 0.09	1.07 ± 0.17	**0.06 ± 0.03**	ns	0.47 ± 0.31	**0.32 ± 0.08**	0.93 ± 0.04	0.83 ± 0.08
2016	0.79 ± 0.01	**0.18 ± 0.06**	0.79 ± 0.16	0.88 ± 0.01	**ns**	ns	0.87 ± 0.01	**0.18 ± 0.05**	0.65 ± 0.12
2020	0.68 ± 0.02	0.78 ± 0.01	**0.08 ± 0.05**	0.67 ± 0.02	0.80 ± 0.01	**0.07 ± 0.04**	0.73 ± 0.02	0.75 ± 0.01	**0.17 ± 0.05**

between Drummartin and Condobolin was also very high with similar standard errors (1.03 ± 0.37). The other coppice cross-site correlations were inflated well above one, due to weak additive variances used for these estimates and should be used with caution. All genetic correlations were not significantly different from unity ($P > 0.05$).

Estimated gains following selection

Condobolin displayed the highest estimated gains for the 3-year sapling and coppice assessments with 24.1% and 14.8%, respectively (Table 8). Gains were similar for 3- and 6-year sapling at Newdegate with 17.2% to 17.7%, respectively and for 6-year sapling at Condobolin (16.5%). Gains were substantially lower for coppice at Newdegate (9.5%) and Drummartin (8.4%) which also had the lowest 3-year sapling gain of 11.5%. When applying the 3-year selections to the 6-year assessment, gains were reduced by about 13% at Condobolin and 3% at Newdegate. However, simulating the gains if 3-year sapling selections were applied to coppice, negative gains were observed for both sites (−6.2% and −7.1%) with positive but small gains at Drummartin. Repeating the simulation and assuming selection had been conducted in 6-year saplings immediately prior to harvest, positive gains were observed for coppice (6.4% to 9.3%) but these were smaller gains at each site than when selection was conducted and applied to the coppice (8.4% to 14.8%).

With fewer trees selected for clonal selection, gains were higher than for the orchard thinning scenario, with gains for saplings (24.6% to 65.3%) and coppice (18.9% to 37.2%) assessments. Similar trends were also observed when applying selections to other assessments, but the magnitude of gains was larger. When 3-year sapling selections were applied to coppice, gains were reduced by 10.7% at Drummartin, 36.0% at Newdegate and 51.4% at Condobolin when compared to coppice selections applied to coppice.

Comparison of the number of individuals selected from each family post-selection (Tables S5, S6 and S7) revealed four broad performance categories. These were (1) elite families across all assessments, (2) poor performing families across all assessments, (3) strong sapling but poor coppice performers and (4) weak sapling but strong coppice performers. By far, the most numerous category was elite families with 27 families at Newdegate and Drummartin and 25 families at Condobolin maintaining their full complement of possible selections across all assessments (e.g. families 7, 11 and 14). In contrast, selection completely eliminated seven families at Newdegate and five at Condobolin (e.g. families 30, 58, 59 and 66). At Newdegate and Condobolin, families 10 and 61 had the full sapling complement selected (or one eliminated) but no coppice selected, whereas families 17 and 54 performed poorly as saplings yet well after the coppice assessment. At Newdegate, family 48 was eliminated for sapling

Table 7 Heritabilities, cross-site and genetic correlations ± standard errors for the 3- and 6-year sapling biomass assessments (2013 and 2016) and coppice assessment (2020) from the three mallee progeny trials. Heritabilities on the diagonal (in bold); genetic correlations off-diagonal. ns denotes non-significant additive variance. Trial names Newde, Drum and Condo refer to Newdegate, Drummartin and Condobolin, respectively

	2013			2016			2020		
	Newde	Drum	Condo	Newde	Drum	Condo	Newde	Drum	Condo
Newde	**0.19 ± 0.07**	1.11 ± 0.37	0.82 ± 0.15	**0.18 ± 0.06**	ns	0.94 ± 0.13	**0.07 ± 0.05**	1.45 ± 0.49	0.93 ± 0.31
Drum		**0.05 ± 0.03**	1.03 ± 0.32		**ns**	ns		**0.07 ± 0.04**	1.21 ± 0.25
Condo			**0.32 ± 0.08**			**0.21 ± 0.06**			**0.19 ± 0.05**

Table 8 Gains made from selection to produce a thinned seed orchard or clonal orchard using data from the three biomass assessments: 3- and 6-year sapling and coppice at Newdegate and Condobolin, and the 3-year sapling and coppice assessment at Drummartin. Gains were calculated from the selections made in 3-year sapling assessments and applied to the 6-year sapling assessment. Gains were also calculated for coppice biomass assuming selections had been conducted in both 3-year and 6-year saplings. The number of trees selected for thinning at Newdegate (n = 171–185), Condobolin (n = 262–284) and Drummartin (n = 238–240), and for clonal population n = 10

Trial	Selection	3-year sapling gain (%)	6-year sapling gain (%)	Coppice gain (%)	6-year gain using 3-year selections (%)	Coppice gain using 3-year selections (%)	Coppice gain using 6-year selections (%)
Newdegate	Thinning	17.2	17.7	9.5	13.8	−6.2	6.4
Condobolin		24.1	16.5	14.8	11.3	−7.1	9.3
Drummartin		11.5		8.4		3.4	
Newdegate	Clonal	40.4	41.3	22.6	26.9	−13.4	15.4
Condobolin		65.3	40.6	37.2	35.3	−14.2	19.8
Drummartin		24.6		18.9		8.2	

selections yet the full complement of coppice was selected, and this also occurred with family 25 at Condobolin.

A similar trend held for the clonal selections (Table 8): there were four families that were selected seven or more times out of eight possible selection opportunities (families 11, 19, 41 and 46) (Table S8). Twenty-two families were only selected as sapling whereas eight families were only selected as coppice. Out of the 66 families present in the progeny trials, 36 were not represented for clonal propagation.

Discussion

This study shows that across the three trials, almost all *E. polybractea* saplings coppiced following harvest. From the populations used in this study, coppicing seems to be a widespread adaptation suggesting that coppicing is strongly linked to the species fitness. There were some large differences in the performances of certain families when comparing the sapling to the coppice assessments. Heritabilities were weak to moderate for all biomass assessments and reduced from first sapling assessment to coppice assessment at Condobolin and Newdegate but increased at Drummartin. Strong within-site phenotypic correlations were observed at all trials with high genetic correlations at the trials with significant additive variance. Within years, cross-site genetic correlations were strong between the trials. Gains were highest for the sapling biomass and reduced for coppice, but if used as a short-rotation coppice crop, selection should be done on the coppice assessment.

Considerable variation of growth rates was observed across the three trials. Condobolin experienced the fastest growth before the 3-year sapling assessment with the slowest growth at Newdegate. Part of elevated growth rates at Condobolin may be explained by the manual watering post-planting, whereas Newdegate receiving about 900 mm less rainfall over the 3 years than the other two sites. However, by the 6-year sapling assessment, tree sizes across the three trials were similar

suggesting that the Condobolin may have experienced competition-related growth suppression. The average size of the coppice at Drummartin was more than double that of the other two sites, but over the period, Drummartin received an additional 100 mm of rainfall with the lowest evaporation rates.

Survival

Previous work has reported that survival from trials at multiple locations in WA, Victoria and NSW and under varying numbers of harvests was generally high, ranging from 90 to 99% (Goodger et al. 2007; Milthorpe et al. 1998; Milthorpe et al. 1994; Spencer et al. 2019; Wildy et al. 2000). In our study, survival was at the higher range recorded for this species. Various factors, including family (Whittock et al. 2003), environment (Spencer et al. 2019; Wildy et al. 2000), harvest timing and frequency (Spencer et al. 2019; Wildy and Pate 2002) can contribute to mortality across studies. The seed for the relatively low (90%) survival reported in Goodger et al. (2007) was from central Victoria whereas in our study, the families were collected from parent trees located in a disjunct south-central NSW population, several hundred kilometres to the northeast. It is possible that the origin of parent trees (environmental adaptation) contributes to resprouting capacity; however, it is more likely that the age at first harvest is responsible for the difference in survival with the harvest age between 1 and 3.5 years old from the trials with lower survival (Goodger et al. 2007; Milthorpe et al. 1998; Milthorpe et al. 1994; Wildy et al. 2000). In this present experiment, the mallee were 6 years old and between 5- and 10-year-old trees at first harvest in Spencer et al. (2019). We found no evidence that population differences contributed to survival following harvest.

We found that larger *E. polybractea* saplings were more likely to coppice than smaller saplings. In contrast, Wildy et al. (2000) found for the same species that coppice success is not related to the size of the sapling prior to harvest. These divergent results may be explained by the age and planting

configuration in our study with older trees subjected to block planting configuration compared to alley planting used by Wildy et al. (2000). Both of these factors increase competition between trees suppressing smaller trees, which were less likely to reshoot. Whittock et al. (2003) found in agreement with our study, for *E. globulus*, that coppice success was determined by the size of sapling prior to harvest ($r_g = 0.61$). For *E. kochii*, Wildy and Pate (2002) found that coppice success is not due to starch reserves or the number of meristematic foci in the lignotubers.

Genetic parameters

Heritability of sapling biomass is generally low to moderate for semi-arid mallee eucalypt species (Mazanec et al. 2020; Mazanec et al. 2017; Spencer et al. 2020); however, nothing has been published regarding the heritability of coppice production of *E. polybractea*. The heritability of resprouting following harvest for other eucalypt species has been estimated. For example, the diameter at breast height of *E. dunnii* coppice has been recorded as $h^2 = 0.42 \pm 0.17$ (Li et al. 2012) and a range of $h^2 = 0.33$ to 0.57 for *E. grandis* (Reddy and Rockwood 1989). Much lower heritabilities ($h^2 = 0.16 \pm 0.05$) were found for coppice height for *E. globulus* in Tasmania which is closer to the range found in the present study (Whittock et al. 2003).

At Newdegate, the two heritability estimates for saplings were stable but lower for coppice. At Condobolin, there was a large drop between the first and second sapling heritability estimates and a further, but smaller, drop in the coppice cycle. At Drummartin, the heritability of coppice was higher than for the two sapling assessments. The reason for the divergent trends in heritability between sites is unclear and may be driven by the different environmental conditions at the three trials and contrasts with the findings from Osorio et al. (2001) who found for *E. grandis* that heritabilities of tree volume and mean annual increments increased from 3 years old until 6 years old (harvest age). It was, however, expected that there would be divergence of performance in a mallee between the sapling and coppice assessments, on the basis of genetic control of lignotuber development in other eucalypt species (Bortoloto et al. 2020; Walters et al. 2005; Whittock et al. 2003).

Heritability of below 0.1 renders selection of good genotypes unreliable (Cotterill and Dean 1990) which is of concern for selection of coppice at Newdegate and Drummartin. The timing of measurement may influence heritability estimates. The coppice were below the size likely to be profitable for harvest especially at Newdegate and Condobolin where the average coppice was under 12 kg (Spinelli et al. 2014). These trials should be assessed immediately prior to harvest of the first coppice cycle as differentiation between families may increase with age. If heritability estimates are not improved, then it may be necessary to use backward selection

as this enables calculation of parental breeding values with high accuracy (Falconer and Mackay 1996; Isik et al. 2017).

Across all trials, there were moderate to high positive phenotypic correlations between the three biomass estimations indicating that bigger saplings, either at age 3 or 6 years, will produce bigger coppice. This is contrary to the finding from the selection scenarios that show that selection for 3-year-old saplings will result in a negative gain for coppice production. However, across all trials, the phenotypic correlations were weakest between the first sapling and the coppice estimates. These correlations were similar to the Pearson's correlation found between sapling and coppice biomass for *E. polybractea* of $r = 0.73$ which reduced to $r = 0.66$ between two coppice cycles (Goodger et al. 2007). This indicates that, if selecting for coppice biomass using sapling data, selections are best done on older saplings, which are less likely to be affected by nursery or planting effects.

Across the three *E. polybractea* trials, within-site genetic correlations revealed similarities and differences when compared to the phenotypic correlations. Excluding the Drummartin trial (due to non-significant or weak sapling additive variance), strong and positive genetic correlations were estimated between the sapling (3 and 6 years) and the coppice biomass estimates indicating that similar genes are associated with sapling and coppice growth (Falconer and Mackay 1996). However, contrary to the phenotypic correlations, there were stronger genetic correlations between the first sapling estimate and the coppice estimate at Newdegate (1.07 ± 0.17) and Condobolin (0.86 ± 0.07) than between the second sapling assessment and coppice (Newdegate (0.79 ± 0.14) and Condobolin (0.67 ± 0.11)) but these were either within or close to the margins of error. Similar magnitude of genetic correlations have been found for *E. dunnii* in China (Li et al. 2012). Contrary to these findings, Whittock et al. (2003) found much weaker correlations between diameter of sapling and the height of coppice ($r_g = 0.12$). Such divergence may arise from the substantial difference between subraces of *E. globulus* in lignotuber size and development which led to a much lower proportion of coppice success across the species distribution (Whittock et al. 2003). Similar results were observed by Walters et al. (2005) for *E. obliqua* who found a provenance response to lignotuber size. *E. obliqua* and *E. globulus* are able to regenerate from seed or coppicing from lignotubers, but it seems that certain provenances favour either method. Mallee eucalypts invest in more below-ground biomass than non-mallee species, with *E. polybractea* having root to shoot ratio of 0.61 (Brooksbank and Goodwin in press) which is substantially higher than *E. globulus* with 0.29 to 0.30 (Fabião et al. 1995; Resh et al. 2003). This additional investment in below-ground biomass allows almost all *E. polybractea* saplings to reshoot, unlike *E. obliqua* and *E. globulus*.

There is some debate as to whether selections should be done on first (sapling) or second (coppice) rotations for

coppice crops. A study of five experiments of mixed eucalypt species in Brazil demonstrated that selection before the first rotation was appropriate (Amâncio et al. 2020). This is contrasted with the results from a small *E. polybractea* trial that suggests that selection for biomass at first coppice rotation is better than when done at saplings or after the second coppice rotation (Goodger et al. 2007). Studies with the aim of quantifying the best rotation for biomass selection of coppice crops are rare, but our results are in agreement that second rotation data should be used.

At Drummartin, the additive variance became significant after harvest suggesting that the genes associated with coppicing were more strongly expressed than for either of the sapling assessments that either had very weak or non-significant additive variance. Low additive variance resulting in low or no heritability suggests there is little differentiation between families. The higher differentiation between families post-coppicing at Drummartin seems to be an anomaly and was not repeated at the other two trials. This suggests that another factor is operating and may be explained, in part, by the genetic control of lignotuber development in some eucalypts species (Bortoloto et al. 2020; Walters et al. 2005; Whittock et al. 2003). Walters et al. (2005) demonstrated in a nursery experiment that *E. obliqua* with larger lignotubers had higher concentrations of carbohydrates and after decapitation, produced more above-ground biomass. If the same mechanism was responsible for coppice regrowth for *E. polybractea*, the higher heritability of coppice growth at Drummartin may actually be indirect measure of the heritability of lignotuber development. However, why this trend was observed at Drummartin and not the other trials is unclear; possibly peculiar site conditions triggered different genes which give rise to more detectable additive variance.

Genotype by environment interactions

The genotype by environment cross-site analysis for this study was partly compromised due to non-significant additive variance for the 6-year sapling assessments at Drummartin and the weakly significant additive variance for the coppice assessment at Newdegate. This resulted in inflated estimates of cross-site genetic correlations for Drummartin with the other trials, especially for the coppice assessments. Being limited to two sites with significant additive variance for all three biomass assessments is not ideal for cross-site analysis and these results should be taken with some caution until confirmed on more sites or further assessments of coppice biomass. However, genetic correlations between Newdegate and Condobolin trials were positive and very strong ($r_g = 0.80$ to 0.94) for all three assessments. There is conjecture from different studies regarding the threshold of cross-site genetic correlations necessary for separate trials into different breeding programmes to maximise biomass gains (Li et al. 2017).

However, Robertson (1959) suggested a threshold of <0.80 to indicate practical significance of G × E interaction, whereas Xie (2003) suggested a threshold of 0.70. Our results suggest that G × E between the Newdegate and Condobolin trials, although having quite different soils and climates, is of little practical significance.

It is clear that the sapling phase in a commercial mallee plantation forms only a small fraction of the productive life of the trees, with the vast majority of biomass produced in successive coppice cycles (Bartle and Abadi 2010; Davis 2002; Spencer et al. 2019). The results of this study combined with that of Goodger et al. (2007) indicate that maximum gains in biomass production in the first coppice cycle are likely to be achieved by selecting seed orchard parents after the first coppice cycle. Some caution is required and additional measurements in subsequent coppice cycles are required to confirm this result. These findings dictate that considerable time is required to establish an improved seed orchard suitable for coppice production from wild *E. polybractea* parents, with first thinning at a minimum of 5–6 years then a further 3–4 years for coppice assessment, then an additional 3–4 years to produce usable seed. However, this process may be hastened by thinning the three progeny trials into seed orchards based on coppice selections, or by producing elite clonal orchards using coppice shoots (Goodger et al. 2008) which would hasten improved seed for a biomass industries.

Conclusions

This study found that *E. polybractea* coppices vigorously after harvesting with very low mortality. Due to the uneven number of families in each population, little is gained from further analysis, but generally, populations that performed well did so across the three trials and the three assessments. Inspection of the performance of the individual families revealed that certain families seem to be disposed to either sapling or coppice production. However, more than half the families were stable across the three biomass assessments, with consistently high or low yields.

We found similar genetic parameters to other studies of mallee, with low to moderate heritabilities of biomass estimates. However, this study is unique because it includes biomass estimates of both sapling and coppice. Strong within-site genetic and phenotypic correlations were established between sapling and coppice biomass estimates across two of the three trials suggesting that selections of superior saplings or coppice would result in biomass gains. The cross-sites genetic correlations, where additive variance was significant, revealed that G × E was likely to be of little practical significance. If *E. polybractea* is to be used for long-term short-rotation coppice crops, selection for breeding may best be conducted in the first or subsequent coppice cycles. Assessment of additional

coppice cycles is necessary to confirm at what point selection is optimal. Due to the low additive variance for the coppice assessments at Drummartin and Newdegate, a further harvest and reassessment of biomass after 3–4 years of growth may yield improved estimates of genetic parameters at these sites with the potential for further biomass gains. These trials may be thinned to produce improved seed orchards or elite individuals could be used for explant sources for clonal orchards. This will result in enhanced biomass production of *E. polybractea* which will benefit commercial plantations.

Declarations

Conflict of interest The authors declare no competing interests.

Data archiving statement Biomass estimates from this manuscript have not been currently achieved, but prior to publication, these data will be published on CSIRO data access portal with a DOI number https://data.csiro.au/dap/home?execution=e1s1.

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