



# Testing allometric equations for prediction of above-ground biomass of mallee eucalypts in southern Australia



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## ABSTRACT

In medium-low (250–850 mm year<sup>−1</sup>) rainfall regions of southern Australia, reforestation with mallee eucalypts is promoted for biomass production for carbon sequestration and/or bioenergy. Cost-effective estimation of biomass is essential for assessing the economic viability of plantings. To explore this, we collated biomass data from 198 stands in southern Australia ( $N = 3384$  individual trees, including 1065 trees re-grown as coppice) and developed allometric equations for non-destructive estimation of above-ground biomass based on either stem diameter at 10 cm height for uncut trees, or on crown volume index for coppiced trees. Three classes of allometric equations were developed. In order of decreasing specificity, these were; (i) site-and-species specific, (ii) generic species-specific, and (iii) generic multi-species. Validation at the site level was realised by analysing the bias, precision and overall accuracy of allometry-predicted biomass when tested against directly-measured biomass harvested manually from whole-plots across six contrasting sites. Another 17 plantings were harvested with a mechanical harvester. A finer-scale analysis investigating the performance of these allometric equations at the individual-tree level across all stands was also undertaken. When predicting biomass at the site-level using either of the generalised equations, the percentage error of prediction was  $< \pm 9\%$ , but could be in the range of  $\pm 15\%$  to  $\pm 21\%$  at individual sites. Precision, and thus accuracy, increased slightly with the level of specificity of equations. Although allometry was statistically significantly influenced by climate, inclusion of the site-specific factor of average rainfall in generic equations increased efficiency of prediction of above-ground biomass by only 5%. We conclude: (i) site-and-species specific equations are more accurate than generic equations for predictions at the site-level, and (ii) generic equations, particularly species-specific relationships, can be confidently applied to provide regional, or estate-level, estimates of above-ground biomass across a range of mallee eucalypt plantings in the medium-low rainfall regions of southern Australia.

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## 1. Introduction

New tree plantings established for procuring carbon offsets in southern Australia are mostly in the medium-low rainfall zone

receiving 250–850 mm rain year<sup>−1</sup>, where low land values make reforestation viable (Petersen et al., 2003; Bartle et al., 2007; Wu et al., 2008; Yu et al., 2009; Polglase et al., 2011; Paul et al., 2013a). Much of this reforestation is with mallee eucalypts (Mitchell et al., 2012). In addition, substantial areas of mallee eucalypts have been established over the last 10–15 years for biomass used for bioenergy, activated carbon, charcoal, and composite wood products (OMA, 2008). Mallee eucalypts have

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multiple woody stems arising from an underground lignotuber, and they coppice readily (Jacobs, 1955). Land managers have often preferred mallee eucalypts over other woody species, as they can be integrated into farms, often in narrow belts allowing cropping or pasture production in-between belts. Biomass production offers income in addition to those from a carbon market.

Landowners are now assessing whether the economic value of maintaining mallee plantings unharvested for carbon outweighs that from harvested biomass with less long-term average carbon stocks. A key factor in this decision will be the estimated rates of biomass accumulation. As a biomass industry develops, estimates of above-ground biomass will become increasingly common as biomass from whole plots of mallee plantings are operationally harvested and weighed to sell. However, such data are not widely available because the market for biomass is still in its infancy; most mallee plantings are still relatively young (Paul et al., 2013b) and operational harvesting for biomass products is unlikely to be viable in regions of low productivity (rainfall 250–450 mm year<sup>-1</sup>) (Bartle et al., 2012). Eucalypt plantings in such environments require cost-effective non-destructive methods for estimating above-ground biomass.

A common non-destructive method of biomass estimation in forests is the application of allometric relationships between stem diameter and biomass. Most published allometric equations for above-ground biomass of mallee eucalypt plantings are specific for either a site (Carter et al., 2008), or to limited number (2–19) of sites within specific regions of Western Australia (Grove et al., 2007; Huxtable et al., 2012; Brooksbank and Goodwin, 2012). It is often neither practical nor cost-effective to develop site-specific allometric equations at each new site, or small clusters of sites. General allometric equations based on large numbers of sites may be useful when biomass estimates are required for a specified estate or region which includes a range of stand ages, geographic/climatic environments, and management regimes. Development of these generalised equations for mallee plantings would increase the cost-effectiveness of field-based measures of biomass across sites.

Previous studies (Montagu et al., 2005; Williams et al., 2005; van Breugel et al., 2011) have shown high variation in residuals of prediction of above-ground biomass when using generic as opposed to site-specific equations. However, as generic equations are based on a range of sites with larger sample numbers than site-specific equations, they have a lower risk of average bias when applied across sites. Thus, when tested against direct measures of above-ground biomass, Paul et al. (2013) found that the average bias of predictions across eight contrasting planting sites was low (<±11%).

The objective of this study was to test whether generic allometric equations are adequate for predicting above-ground biomass of uncut and coppiced mallee eucalypt plantings in southern Australia, and if so, whether these equations can be generalised across sites, climatic regions, and/or species. This was done by comparing the precision, bias, and accuracy of predictions of biomass made at the site-level using generic multi-species, generic species-specific and site-and-species specific allometric equations, when all three classes of equations are tested against biomass determined directly through whole-plot harvesting.

## 2. Methods

### 2.1. Study sites and data collection

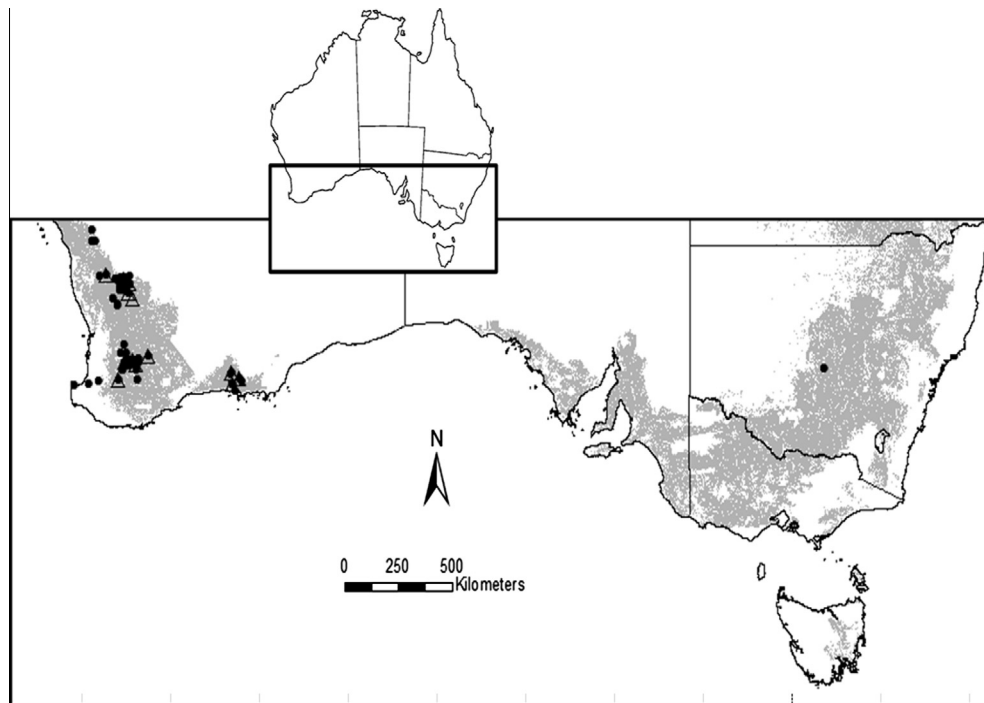
Our domain of study was for young (<16-year-old uncut and <5-year-old coppiced) mallee eucalypt trees which generally had good initial rates of survival in regions of southern Australia where rainfall is 250–850 mm year<sup>-1</sup>. For both uncut and coppiced mallee

eucalypt trees across 198 sites within this domain, we collated a total of 3384 observations on stem diameter and above-ground biomass of individual trees for development of allometric equations for three species currently planted: (i) *Eucalyptus kochii*, including the sub-species of ssp. *kochii* Maiden & Blakely, ssp. *borealis* C.A. Gardner, and ssp. *plenissima* C.A. Gardner (grouped in the text as *E. kochii*, oil mallee), (ii) *Eucalyptus loxophleba* ssp. *lissophloia* L.A.S. Johnson & K.D. Hill (smooth bark york gum), and (iii) *Eucalyptus polybractea* R.T. Baker (blue mallee) (Table 1 and Fig. 1). These species differ substantially in their growth forms, with *E. kochii* tending to produce the most stems, and *E. loxophleba* ssp. *lissophloia* tending to produce the fewest stems. In addition to the data collated from several existing studies (Table 1), we harvested biomass at the plot level at 22 sites (Table 2). To validate estimated biomass using three different classes of allometric

**Table 1**

Details of collated datasets on individual tree above-ground biomass from uncut and coppiced mallee eucalypts, including numbers of sites measured (where a site is defined as a planting of common age and treatment, and so includes treatments from within the one planting), the number of trees measured for biomass and stem diameter, and the range in mean annual rainfall (MAR) across the sites from which the trees were harvested.

Sites	Trees	MAR (mm year <sup>-1</sup> )	Source
<i>Uncut E. kochii</i>			
7	157	299–303	Peck et al. (2012)
6	108	243–355	Wildy, D., unpublished data
5	47	326–353	Ritson, P., unpublished data
7	35	325	Grove et al. (2007)
1	18	334	Carter et al. (2008)
1	9	463	Brooksbank and Goodwin (2012)
<i>Uncut E. loxophleba</i> (low rainfall, 250–400 mm)			
26	449	284–357	Peck et al. (2012)
5	217	311–364	This study
6	106	276–355	Wildy, D., unpublished data
14	73	325–382	Grove et al. (2007)
3	30	327–371	Ritson, P., unpublished data
2	23	380	Brooksbank and Goodwin (2012)
<i>Uncut E. loxophleba</i> (high rainfall, 400–850 mm)			
6	113	418–501	Peck et al. (2012)
2	36	774–825	Wildy, D., unpublished data
2	20	409–416	Ritson, P., unpublished data
1	10	416	Brooksbank and Goodwin (2012)
<i>Uncut E. polybractea</i> (low rainfall, 250–400 mm)			
2	107	378	This study
14	75	335–375	Brooksbank and Bevan (2010)
1	124	323	Brooksbank and Goodwin (2012)
5	90	346–354	Wildy, D., unpublished data
6	31	382	Grove et al. (2007)
2	27	333	Peck et al. (2012)
2	25	382	Bennett, R., unpublished data
1	10	378	Ritson, P., unpublished data
<i>Uncut E. polybractea</i> (high rainfall, 400–850 mm)			
11	250	404–526	Peck et al. (2012)
2	36	774–786	Wildy, D., unpublished data
2	32	416–524	Brooksbank and Goodwin (2012)
2	30	425–437	Ritson, P., unpublished data
2	20	487	Sudmeyer et al. (2008)
1	11	497	Sudmeyer and Daniels (2010)
<i>Coppiced E. kochii</i>			
7	103	312–315	Peck et al. (2012)
10	93	372	Wildy and Pate (2002), Wildy (2003)
1	76	416	Sudmeyer, R., unpublished data
<i>Coppiced E. loxophleba</i>			
19	448	308–429	Peck et al. (2012)
<i>Coppiced E. polybractea</i>			
13	325	343–530	Peck et al. (2012)
1	20	380	Sudmeyer, R., unpublished data
147	2319	–	Total (uncut trees only)
198	3384	–	Total (all trees)



**Fig. 1.** Location of sites where uncut (●) and coppiced (△) trees were sampled for above-ground biomass. Shaded area represents area of Australia where the generic allometric equations are applicable; cleared areas of Australia where mean rainfall is 250–850 mm year<sup>-1</sup>.

equations, site-level predictions of biomass made through application of these equations were tested against measurements of biomass attained through whole-plot harvesting. At six of these sites all trees within plots were harvested manually, while at the remaining sites a mechanical harvester/chipper was used. At the Brothererony 1 site, both types of harvesting were undertaken.

At manually harvested sites (Table 2), stems were cut at 5–10 cm above the ground (with a few exceptions, see Section 2.3), on a tree-by-tree basis. Biomass from all trees within the plots was weighed fresh (accuracy ca.  $\pm 0.01\%$  on a 150 kg load cell). Moisture contents were calculated for components and used to calculate the dry weight. Fresh weights were measured for: (i) live crown (all foliage, twigs and branches <20 mm diameter), (ii) live bole (stems and branches to 20 mm diameter), and (iii) dead branches and stems. Representative sub-samples (ca. 300–800 g, with an accuracy of ca.  $\pm 0.09\%$  on a 15 kg balance) of each were oven-dried at 70 °C to constant weight. The biomass of each tree was summed to obtain total biomass per plot, and averaged to obtain site-level information.

At sites where trees were harvested by mechanical harvester and chipper (Paterson, 2012), the chips were collected into a weigh bin which had a 10,000 kg capacity load cell ( $\pm 1$  kg). To avoid damage to the harvester, stems were cut at about 10 cm above the ground. Biomass above the 10 cm stump was taken as total above-ground biomass. To determine moisture content, sub-samples were taken from the well mixed chipped biomass. The number of sub-samples (ca. 6 kg each) varied between 3 and 40, depending on the number of trees harvested at the site. They were weighed fresh using a 15 kg load cell ( $\pm 0.5$  g) and oven-dried at 70 °C to constant weight. The percentage moisture content was used to calculate dry weight.

## 2.2. Measurement of explanatory variables: stem diameter, height and crown volume index

For uncut (non-coppiced) trees, stem diameter was used as the independent explanatory variable in the allometric equations.

Mallee eucalypts are multi-stemmed and diameter was measured on each stem at 10 cm above the ground (D10). For all trees an equivalent of diameter was calculated for multi-stemmed individuals ( $D_i$ ) to obtain an equivalent single diameter, cm,  $D_e = \sqrt{\sum D_i^2}$ . This equivalent diameter was used in equations (and subsequently referred to as D10), and for the calculation of stocking rates (Table 2).

When harvested manually, the stem diameter of each tree was measured. For sites harvested with the harvester, diameter measurements were not always taken from the same trees harvested. This was because some of the inventory plots where stem diameters had been measured were unsuitable for the mechanical harvester due to access or safety concerns. This variation was assumed to be of little importance given that, for all 81 plots measured across the 17 sites, average standard deviation of stem diameter was only 2.4 cm (mean 7.2 cm).

Trees which had been coppiced in less than 5 years had numerous small stems and a growth habit different to uncut trees. This made stem diameter measurement difficult and an alternative tree variable was required. Additional explanatory variables were tested: (i) tree height, and (ii) crown volume index (CVI, m<sup>3</sup>), calculated as the product of tree height, canopy width measured parallel to the planting rows and canopy width measured perpendicular to the planting rows (Huxtable et al., 2012). We compared the two alternative variables in terms of the EF (model efficiency, see Section 2.6) generated from their respective allometric equations.

## 2.3. Data consistency

When developing generic equations, caution is required to ensure that biomass datasets collated from multiple sites, using different harvesting protocols, are comparable. There were three issues to be addressed: (i) the height at which stem diameter was measured, (ii) the height above the ground at which trees were cut, and (iii) variation in moisture content and their effect on fresh-to-dry weight ratios.

**Table 2**

Summary of the main site characteristics, including harvesting method (manual, M, or mechanically/operational, O), location (latitude, longitude, in decimal degrees), observed above-ground biomass ( $\text{Mg ha}^{-1}$ ), site mean annual rainfall (MAR), plot area and number (Plot N), stand density (trees per hectare), site average basal area (BA), number of trees measured (Tree N), age of planting at time of measurement, and the species.

Site	Har-vest type	Location (decimal degrees)	Obs. biomass ( $\text{Mg ha}^{-1}$ )	MAR (mm)	Plot area (ha)	Plot N	Stocking (trees $\text{ha}^{-1}$ )	BA ( $\text{m}^2 \text{ha}^{-1}$ )	Stand density (trees $\text{ha}^{-1}$ )	Tree N	Age (yrs)	Species
Pepal	M	–33.4865, 117.7912	20.87	406	0.04	3	1863	8.71	77	77	11	<i>E. loxophleba</i>
Bird	M	–32.8515, 117.5892	37.68	376	0.03	3	1356	11.92	41	38	11	<i>E. loxophleba</i>
Quicke	M	–32.6736, 118.2361	77.63	339	0.02	3	1894	25.55	29	29	14	<i>E. loxophleba</i>
Temby	M	–33.1457, 117.7187	22.61	353	0.03	3	1433	6.92	44	43	16	<i>E. loxophleba</i>
Angel	M	–30.1970, 117.1160	9.93	297	0.03	3	1100	3.45	34	33	16	<i>E. loxophleba</i>
Brotherony 1	M/O	–33.1368, 146.6380	20.60	378	0.03	6	1233	4.92	255	61	7	<i>E. polybractea</i>
Wycheproof 1	O	–36.1760, 143.3803	11.51	365	0.07	4	943	3.7	275	275	7	<i>E. polybractea</i>
Wycheproof 2	O	–36.1760, 143.3803	15.81	365	0.07	4	946	4.76	267	267	7	<i>E. loxophleba</i>
Carmody	O	–36.1602, 143.4044	16.10	366	0.03	10	1283	4.52	385	285	7	<i>E. polybractea</i>
Batters 1	O	–36.5019, 143.2934	20.17	415	0.05	4	1949	11.79	392	392	7	<i>E. polybractea</i>
Batters 2	O	–36.5019, 143.2934	17.40	415	0.04	6	1912	5.96	479	479	7	<i>E. loxophleba</i>
SW Watts 1	O	–36.3996, 143.3102	24.08	379	0.03	4	1511	6.62	204	204	8	<i>E. polybractea</i>
SW Watts 2	O	–36.3996, 143.3102	25.11	379	0.06	4	1511	7.01	340	340	8	<i>E. loxophleba</i>
N Watts	O	–36.3996, 143.3102	21.42	379	0.09	3	2122	10.23	565	565	8	<i>E. polybractea</i>
Campbell 1	O	–36.2668, 143.1047	70.47	373	0.02	3	1533	13.71	117	117	7	<i>E. polybractea</i>
Campbell 2	O	–36.2668, 143.1047	62.64	373	0.02	4	900	9.66	163	163	7	<i>E. loxophleba</i>
Weenya sp3	O	–33.3422, 145.8037	7.64	366	0.04	4	1684	5.39	257	257	7	<i>E. polybractea</i>
Weenya sp4	O	–33.3422, 145.8037	8.58	366	0.03	3	1351	4.38	142	142	7	<i>E. loxophleba</i>
Weenya sp5	O	–33.3422, 145.8037	6.05	366	0.02	2	1085	2.58	38	38	7	<i>E. kochii</i>
Brotherony 2	O	–33.1368, 146.6380	24.30	378	0.06	6	1388	8.54	524	524	7	<i>E. loxophleba</i>
Brotherony 3	O	–33.1368, 146.6380	16.67	378	0.07	5	1344	6.1	462	462	7	<i>E. polybractea</i>
Kalawa	O	–30.8848, 148.6090	29.09	573	0.13	6	2872	13.79	2169	2169	10	<i>E. polybractea</i>

The height at which stem diameters were measured varied between sites based on the heights of the trees and the height at which multiple stems were initiated. At most sites, diameters were measured at D10. At two sites studied, Temby and Angel, diameters were measured at 50 cm above the ground (D50). To make the diameters comparable, a relationship between D50 and D10 was developed (Paul et al., 2013b). This relationship was based on 300 trees. The relationship was;  $D10 = 0.838 D50 + 0.179$  ( $R^2 = 0.94$ ,  $N = 300$ ).

Most trees were harvested at about 5–10 cm above the ground and biomass was defined as the total above-ground biomass minus the biomass of the remaining stump. At the Angel and Temby sites, trees were harvested at ground level and so stump weights were estimated and subtracted from the total measured. To do this, we derived a relationship to explain the proportion of total above-ground biomass which was stump ( $Pr_s$ ), based on the total above-ground biomass ( $T_{AGB}$ , in kg of dry weight). The relationship was;  $Pr_s = 0.081 T_{AGB}^{-0.222}$  ( $R^2 = 0.21$ ,  $P < 0.001$ ,  $N = 250$ ). Although this relationship had an  $R^2$  of only 0.21, average stump weight of total above-ground biomass was only 5% (standard deviation of 1%,  $N = 76$ ).

Data on moisture content were unavailable for a subset of the data; including 32 (4% of the total) *E. polybractea* uncut trees, 33 (3% of the total) *E. loxophleba* uncut trees, and 9 (3% of the total) *E. kochii* uncut trees, and 18 (2% of the total) *E. polybractea* coppiced trees and 76 (28% of the total) *E. kochii* coppiced trees. For these, we assumed the moisture content of biomass was 40.9%, the average observed across all datasets.

#### 2.4. Development of allometric equations for above-ground biomass

Using the collated data (Table 1), three classes of allometric equations were developed for both uncut and coppiced trees; (i) 87 site-and-species specific allometric equations (using only the biomass data from the species present at a given site), developed only for sites where  $N > 7$ , (ii) generic species-specific allometric equations (derived from collating biomass data from one species from multiple sites), developed for each of the three main species of mallee eucalypts, and (iii) generic multi-species allometric

equations (derived from collating biomass data from all species from all sites). The total number of equations fitted to biomass datasets collated in Table 1 was 87 (75 uncut + 12 coppiced) site-and-species specific equations, 6 (3 uncut + 3 coppiced) generic species-specific equations, and 2 (1 uncut + 1 coppiced) generic multi-species equations.

For each of these allometric equations, a power function was used, which has a linear equivalent form:

$$\ln(y) = a' + b \times \ln(x) + e' \quad (1)$$

where  $y$  is the dependent variable (above-ground biomass,  $\text{kg tree}^{-1}$ ),  $x$  is the independent variable (stem diameter in cm for uncut trees, and height in m or CVI in  $\text{m}^3$  for coppiced trees),  $a'$  is the intercept and equals  $\ln(a)$ ,  $b$  is the allometric exponent, and  $e'$  is the error term. Parameters  $a'$  and  $b$  were estimated using linear least-squares. The required logarithmic transformation to linearise the power function also corrected heteroscedasticity. As logarithmic regressions produce inherently biased estimates of biomass following back-transformation from logarithm, bias was corrected using the ratio of arithmetic sample mean and mean of the back-transformed predicted values from the regression as described by Snowdon (1991). The 95% confidence intervals of both the regression, and the prediction interval, were calculated for each equation developed (Picard et al., 2012). The standard deviation of residuals were also calculated ( $sd(e)$ ) for each allometric equation.

When developing generic equations, data were pooled across sites. There is a potential for unequal numbers of observations among sites to result in a particular data cluster from a single site having an undue influence on the overall result of parameter estimation (Bi et al., 2010). To explore the possible impact on parameters  $a'$  and  $b$  of unequal numbers of observations among sites, least sum squares of residuals were also solved using a weighting applied to the residuals based on the number of observations per site. That is, each tree was weighted by  $1/N_i$  where  $N_i$  is the number of trees from Site<sub>*i*</sub>. This was done so that each site had a total weighting of one, thereby ensuring that each site had an equal influence on the fitting of the allometric equation. An assessment of the impact of site-weighting on predictions of biomass was undertaken through a linear regression analysis



between allometry-predictions of biomass made using the site-weighting and non-weighting approaches.

### 2.5. Statistical analysis of allometric equations

We tested, using ANCOVA analyses, whether allometry significantly differed between; (i) species of both uncut and coppiced trees, each with three factors used in this analysis; *E. kochii*, *E. loxophleba*, and *E. polybractea*, and (ii) regions of differing climate for uncut *E. loxophleba* and uncut *E. polybractea*, each with two factors used in this analysis; low and high rainfall categories. A categorical rather than continuous analysis of rainfall was used because one of the planned applications of this work was to utilise these allometric equations for calibration of forest growth and carbon accounting models which require input parameters based on planting categories. To maintain sufficient replication (and therefore confidence) in each category, only two categories of mean annual rainfall were used; 250–400 mm, and 400–850 mm. The 400 mm cut-off was used as it maintained relatively large sample numbers within each category ( $N$  ranging between 220 and 898), and the <400 mm region was noted by industry as the region of most potential area available for planting (OMA, 2008). ANCOVA analyses for assessment of impacts of climate on allometry were only undertaken on relatively large biomass datasets (i.e. uncut *E. loxophleba* where  $N=1,077$ , and uncut *E. polybractea* where  $N=882$ ), and were not undertaken for uncut *E. kochii*, or any of the species in coppiced plantations, given insufficient sample numbers ( $N$  of 272–377) for further sub-dividing these biomass datasets based on climate.

These ANCOVA analyses assessed whether there were statistically significant differences in slope and/or intercepts of the relationship between the log-transformed explanatory variable and log-transformed biomass between different categories of data. Tukey's test was undertaken to determine the least significant differences between these categories. Levene's test was undertaken to confirm homogeneity of variances. The software used for ANCOVA analyses, Levene and Tukey tests was R-Stats version 2.15.2. To add confidence to these ANCOVA results, multiple regression analyses of log-transformed data were also used (in MS Excel) to assess the degree to which including these species or rainfall categories (expressed as dummy variables) increased the explained variation in observed biomass.

### 2.6. Validation of biomass predictions: bias, precision and accuracy

Bias and precision, as well as overall accuracy of predicted biomass at either a site-level or individual tree-level, were quantified by analysis of the residuals ( $e_i$ ):

$$e_i = E_i - O_i \quad (2)$$

where  $E_i$  is the predicted biomass of the observation  $i$ , and  $O_i$  is the measured biomass. The key quantity to assess overall accuracy is the Mean Square Error of Prediction (MSEP,  $\bar{e}^2$ ), which can be partitioned into a precision component and a bias component:

$$MSEP = \bar{e}^2 = \frac{1}{n} \sum_{i=1}^n (e_i)^2 = \text{var}(e) + (\bar{e})^2 \quad (3)$$

where  $\bar{e}$  is the mean of  $n$  residuals and quantifies the bias, and  $\text{var}(e)$  is the variance of the  $n$  residuals and quantifies the precision. For ease of comparison across a range of sites, or individual trees, bias was expressed as a percentage of the observed biomass (%Bias). Precision was expressed as a standard deviation rather than the variance ( $\text{sd}(e)$ ). The %Bias,  $\text{sd}(e)$  and MSEP were all calculated on the log-transformed scale.

Another quantity which was used to assess accuracy was model efficiency index (EF, Soares et al., 1995), defined as:

$$EF = 1 - \frac{\bar{e}^2}{\sigma^2} \quad (4)$$

where  $\sigma^2$  is the mean square deviation of each observation from the mean square of the observations. A model efficiency of 1.0 indicates perfect fit, and a value of 0.0 indicates the predictions are no better than simply using the mean of the observations.

Using biomass predictions from all classes of allometric equations, %Bias,  $\text{sd}(e)$ , MSEP and EF were calculated by comparing predictions with biomass observed at two scales; site-level (where predictions for individual trees within each plot were summed and expressed on a per area basis, and then average across plots within a sites), and individual-tree level (where individual tree biomass predictions were available from a large number of sites).

The primary analyses were at the site-level, whereby the equations for uncut trees were applied to predict average site biomass (i.e. predicted  $\text{Mg ha}^{-1}$ , averaged across plots within each site) at the 22 direct measurement sites (Table 2). These site-level predictions were compared to the site-average biomass actually harvested from across the same plots (i.e. observed  $\text{Mg ha}^{-1}$ , averaged across plots within each site). This analysis provided a direct test of the overall applicability of the allometrics across a broad range of sites. For the six manually-harvested sites, site-level bias and precision were calculated for all three classes of allometric equations. For the 17 mechanically harvested sites, bias and precision of only the generic species and generic multi-species allometric equations could be calculated because of the bulked nature of the sampling. The percentage errors in biomass prediction (%EBP) were calculated from the average percentage difference between predicted and observed site biomass (in  $\text{Mg ha}^{-1}$ ) across these direct measurement sites.

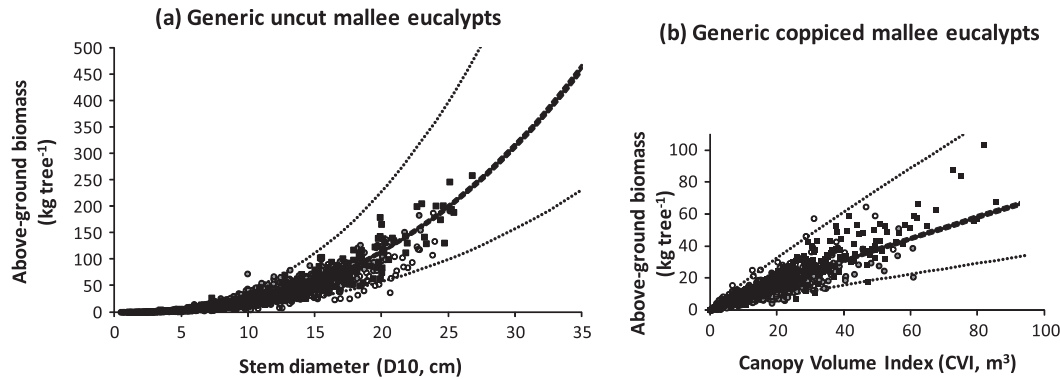
The individual-tree scale analysis utilised all biomass datasets collated (Table 1), and thereby provided a more detailed assessment of the variability in allometric equation performance across a much wider range of sites (i.e. 198 sites as opposed to only 6–22 sites). This analysis entailed a comparison of individual tree's harvested biomass with its predicted biomass attained from the three classes of allometric equations. In this analysis, very small trees of <5 kg were excluded because they contributed relatively little to biomass and caused high residual variance.

## 3. Results and discussion

### 3.1. Development of allometric equations for above-ground biomass

The generic multi-species, generic species-specific, and site-and-species specific equations are shown in Figs. 2–4. The best-fit parameters for equations are given in Table 3. As indicated by the 95% confidence interval in Figs. 2–4, there was a high degree of certainty in model fits to observed data, and thus the ability of equations to precisely predict average biomass across a large number of trees.

Results from Fig. 4 show that lines of prediction of above-ground biomass using site-and-species-specific equations generally varied little from the relevant generic species-specific predictions. However, EFs tended to be slightly higher for site-and-species-specific equations when compared to generic species-specific equations (Table 3). This is to be expected since site-and-species specific equations were based on a small dataset from one site, compared to the collected datasets from across many sites. Although these results suggest that generic multi-site equations are less precise than site-specific equations, testing of this hypothesis is described in the section below.

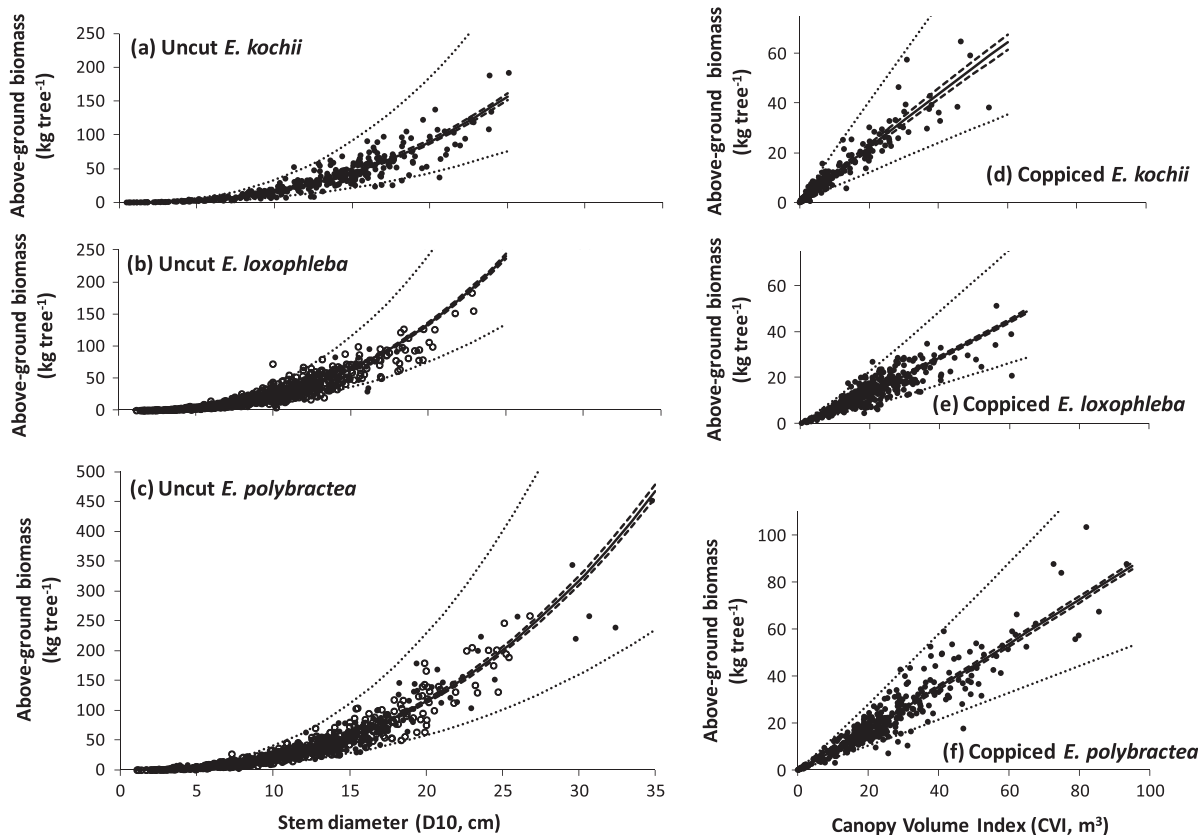


**Fig. 2.** Generic multi-species allometric equations for above-ground biomass of (a) uncut and (b) coppice-harvested mallee eucalypts. Different symbols represent the various classes of species, namely *E. loxophleba* (●), *E. polybractea* (■), and *E. kochii* (○). Parameters for these fitted equations are provided in Table 3. Dashed and dotted lines represent the 95% confidence interval of the regression, and the 95% prediction interval, respectively.

As described below in detail for both uncut and coppiced trees, although allometry was influenced by rainfall, predictions in biomass differed very little across high and low rainfall regions. Further, when using the fitting approach of providing equal weighting between sites, biomass predictions varied little to those obtained using un-weighted fitting approach. A comparison of predicted values on an individual-tree basis using the weighted and un-weighted fitting approaches resulted in slopes of 0.99–1.00 (when forced through the origin), and  $R^2$  of 0.99–1.00, for both uncut and coppiced trees (data not shown). These results confirmed the validity of pooling datasets from across multiple sites to develop generic equations.

### 3.2. Generic allometry for uncut trees

For uncut mallee eucalypts, using diameter as the variable in allometric equations provided a reasonable fit to the data in most cases, with  $EF$  averaging 0.93 (range 0.85–0.99) (Table 3). Other authors have also found that using diameter in allometry-predicted biomass resulted in relatively good fits to data (Brown et al., 1989; Ketterings et al., 2001; Jenkins et al., 2003; Zianis and Mencuccini, 2004; Lambert et al., 2005; Chave et al., 2005; Basuki et al., 2009; Xiang et al., 2011; Kuyah et al., 2012a,b), thereby providing evidence that the simple power-law model based on stem diameter is universal across a wide range of woody species.



**Fig. 3.** Generic species-specific allometric equations for above-ground biomass of uncut *E. kochii* (a), *E. loxophleba* (b) and *E. polybractea* (c), and for coppice-harvested *E. kochii* (d), *E. loxophleba* (e) and *E. polybractea* (f). Parameters for all fitted equations are provided in Table 3. Dashed and dotted lines represent the 95% confidence interval of the regression, and the 95% prediction interval, respectively. In plots (b) and (c), datasets have been divided in approximately half based on mean annual rainfall (i.e. 205–400 mm (○, dash line) or 400–850 mm (●, solid line)).

This is to be expected as they have their origins in common geometric and hydrodynamic principles that govern the transport of essential materials to support cellular metabolism (Enquist et al., 1998; West et al., 1999; Enquist and Niklas, 2001).

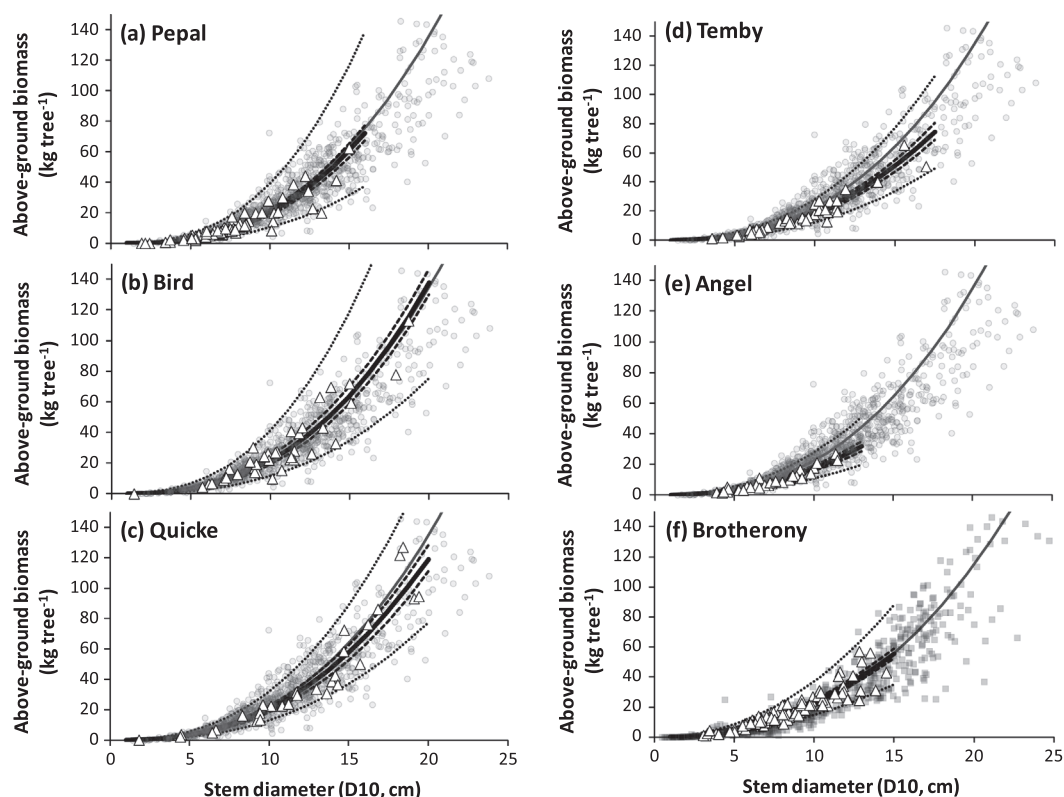
Allometry appeared to be relatively similar between the three species of mallee eucalypts. Thus, when data from these species were pooled together in the generalised multi-species mallee eucalypt equation, it predicted biomass of all trees with a reasonable accuracy, with  $EF$  being 0.94 (Table 3 and Fig. 2a). However, as indicated by the species-specific relationships between of biomass and diameter (Fig. 2a), and confirmed by the ANCOVA analysis, there were differences between species in terms of the relationship between stem diameter and above-ground biomass of uncut trees ( $P < 0.001$ , Table 4). Grove et al. (2007) came to a similar conclusion. Here we found that *E. kochii* had low biomass for a given diameter compared with *E. polybractea* and *E. loxophleba* trees (Fig. 2a). But species differences were minor. Including species increased explained variation in biomass ( $R^2$ ) by  $<1\%$  (data not shown). For generic equations,  $EF$  of prediction was also not consistently higher, although  $sd(e)$  tended to be slightly lower, for species-specific equations when compared to multi-species equations (Table 3).

For uncut *E. polybractea* and *E. loxophleba*, there was also a slight difference between allometry between categories of rainfall (Fig. 3b and c). ANCOVA analysis confirmed both slope and intercepts differed ( $P < 0.03$ ) between these climatic categories (Table 4), although including climatic categories increased the explained variation in biomass ( $R^2$ ) by  $<1\%$ . Thus, like species factors, climate factors explained little more of the variability in biomass than stem diameter alone. There was no significant effect of rainfall on allometric relationships of *E. kochii* ( $P < 0.05$ ), possibly because

89% of the *E. kochii* plantings were in the 250–400 mm rainfall region, thus having relatively little variability in rainfall. Generic species-specific equations were not further segregated based on climate because the difference in allometry between high and low rainfall regions was only minor (Table 4). Consistently, Grove et al. (2007) found that site factors (fertility and region) significantly influenced partitioning of biomass, yet had little impact on total above-ground biomass of mallee eucalypts. Similarly, Paul et al. (2013) found that for mixed-species environmental plantings, average rainfall had little impact on allometry. Although others (Brown et al., 1989; Sternberg and Shoshany, 2001; Drake et al., 2003; Chave et al., 2005; De Walt and Chave, 2004) found allometry differed with climate, this may be attributable to greater magnitude of climatic gradients investigated and/or these stands were older and as such had a higher potential for biomass accumulations to increase with increased rainfall.

### 3.3. Generic allometry for coppiced trees

For coppiced trees, CVI was always used as the explanatory variable as it provided a 0.24 higher  $EF$  of prediction of biomass when compared to using height ( $N = 1065$ , data not shown). However, for three out of four equation classes shown in Table 3,  $EF$  was less for coppiced trees than for uncut trees. This may be partly attributable to measurement error in CVI being much higher than for diameter as calculation of CVI entails the multiplication of three measurement errors – tree height and two measures of canopy width. In densely-stocked plantings, CVI should only be used in the first 5 years post-coppicing while stem numbers are relatively high prior to canopy closure.



**Fig. 4.** Site-and-species-specific allometric equations for above-ground biomass of uncut *E. loxophleba* at the (a) Pepal, (b) Bird, (c) Quicke, (d) Temby, and (e) Angel sites, and of (f) uncut *E. polybractea* at the Brotherony site. Data and the associated fitted specific allometric equation are represented by the open black symbols ( $\Delta$ ) and solid black line, respectively. Open grey symbols ( $\circ$ ) represent the collated biomass datasets for the relevant species, with the generic species-specific allometric equation represented by the grey line. Dashed and dotted lines represent the 95% confidence interval of the regression, and the 95% prediction interval, respectively.

**Table 3**

Parameters and performance of the three different classes of allometry for above-ground biomass of the form  $\ln(y) = a' + b \times \ln(x)$ , where  $y$  is above-ground biomass ( $\text{kg tree}^{-1}$ ),  $x$  is the independent variable (equivalent stem diameter, cm for uncut trees, and CVI for coppiced trees);  $N$ ,  $CF$ ,  $EF$  and  $sd(e)$  refer to the sample number, bias correction factor, model efficiency, and precision expressed as a standard deviation, respectively. All equations fitted were highly significant ( $P < 0.001$ ). Values in parenthesis are the stem diameters below which the equation may be applied.

Species	Explanatory variable	$N$	$a'$	$b$	$CF$	$EF$	$sd(e)$
<i>Generic multi-species allometrics</i>							
Generic uncut (<35 cm)	D10	2319	−2.771	2.503	1.004	0.936	0.353
Generic coppiced (<60 m <sup>3</sup> )	CVI	1065	0.009	0.911	1.065	0.894	0.349
<i>Generic species-specific allometrics</i>							
<i>E. kochii</i> , uncut (<30 cm)	D10	374	−2.951	2.477	1.029	0.956	0.367
<i>E. loxophleba</i> , uncut (<25 cm)	D10	1077	−2.861	2.592	1.045	0.939	0.297
<i>E. polybractea</i> , uncut (<35 cm)	D10	868	−2.806	2.511	1.024	0.940	0.350
<i>E. kochii</i> , coppiced (<55 m <sup>3</sup> )	CVI	272	0.199	0.965	1.015	0.939	0.303
<i>E. loxophleba</i> , coppiced (<60 m <sup>3</sup> )	CVI	448	−0.743	1.104	1.020	0.859	0.262
<i>E. polybractea</i> , coppiced (<95 m <sup>3</sup> )	CVI	345	−0.319	1.043	1.033	0.949	0.251
<i>Selected site-and-species-specific allometrics</i>							
<i>E. loxophleba</i> , Peral	D10	74	−3.211	2.705	0.988	0.988	0.323
<i>E. loxophleba</i> , Bird	D10	38	−3.052	2.664	0.998	0.934	0.297
<i>E. loxophleba</i> , Quicke	D10	29	−2.844	2.533	1.035	0.977	0.202
<i>E. loxophleba</i> , Temby	D10	43	−2.792	2.479	1.005	0.947	0.196
<i>E. loxophleba</i> , Angel	D10	33	−2.487	2.309	1.020	0.916	0.220
<i>E. polybractea</i> , Brotherony 1	D10	61	−1.746	2.124	1.010	0.907	0.229

**Table 4**

ANCOVA results for comparison of allometry between various groupings of the above-ground biomass datasets. Results shown are tests for differences in slope. Where there were no statistically significant differences in slope, differences in intercepts were tested. ANCOVA results were not shown for comparison of allometry between high and low rainfall in coppiced trees, as differences in slope and intercept were not significant ( $P > 0.05$ ).

		DF	SS	MS	F	P-Value
<i>Comparison between three species of uncut mallee eucalypts</i>						
Slope	Diameter	1	4218	4218	4212	<0.001
	Group	2	30	15	14.9	<0.001
	Diameter $\times$ group	2	0	0	0.23	0.80
	Residuals	2333	2336	1		
Intercept	Diameter	1	4218	4218	4215	<0.001
	Group	2	30	15	14.9	<0.001
	Residuals	2335	2336	1		
<i>Comparison between three species of coppiced mallee eucalypts</i>						
Slope	Diameter	1	574	574	7982	<0.001
	Group	2	38.1	19.1	265	<0.001
	Diameter $\times$ group	2	1.1	0.6	7.87	<0.001
	Residuals	892	64.1	0.1		
<i>Comparison between low and high rainfall for uncut E. loxophleba</i>						
Slope	Diameter	1	1489	1489	16,313	<0.001
	Group	1	2.1	2.1	22.3	<0.001
	Diameter $\times$ group	1	2.3	2.3	25.0	<0.001
	Residuals	1114	102	0.1		
<i>Comparison between low and high rainfall for uncut E. polybractea</i>						
Slope	Diameter	1	1697	1697	14,102	<0.001
	Group	1	5.5	5.5	45.9	<0.001
	Diameter $\times$ group	1	0.6	0.6	4.7	0.03
	Residuals	879	106	0.1		

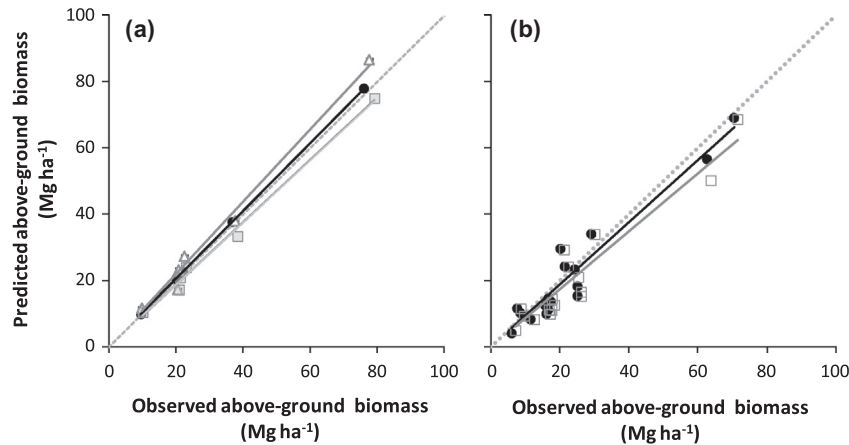
There was no significant ( $P > 0.05$ ) influence of mean annual rainfall on allometry of coppiced trees. ANCOVA analyses for coppiced trees showed significant differences ( $P < 0.001$ , for both slope and intercepts using log-transformed data) between species in their allometry, yet including species increased explained variation in biomass ( $R^2$ ) by <4% (Fig. 2b and Table 4). Further,  $EF$  was not consistently higher for generic species-specific allometry when compared to the generic multi-species allometry, although  $sd(e)$  tended to be slightly lower (Table 3).

#### 3.4. Validation of allometry-predicted biomass

Direct measurement by whole-plot harvesting is a useful means of testing the many allometric equations that are available for forests. However, there have been only three other published studies

which have tested predictions of biomass with direct measures; Arthur et al. (2001) studying northern hardwood forests in the USA; Búquez and Martínez-Yrizar (2011) studying mixed desert species, and Paul et al. (2013) studying mixed-species environmental plantings. This is the first published testing of non-destructive estimates of biomass against direct measures in mallee eucalypts. As expected, there was a near perfect relationship between observed and predicted biomass when site-and-species specific equations are tested at the site for which they were developed (Fig. 5 and Table 5). However, testing also showed that across the range of sites, %EBP was <±9% regardless of the equations used (Fig. 5 and Table 5). Similarly, when tested on an individual tree basis across the wider range of 198 sites, %EBP was consistently low at <±3%. However, when predicting biomass at a given site using either generic equation, %EBP in site-level estimates varied





**Fig. 5.** Comparisons of above-ground biomass estimates ( $\text{Mg ha}^{-1}$ ) from allometric equations with direct (whole-plot harvesting) measures at the: (a) six manually harvested sites using site-and-species-specific allometric equations ( $\bullet$ ,  $y = 1.00x$ ,  $R^2 = 1.00$ ,  $EF = 1.00$ ), generic species-specific allometric equations ( $\triangle$ ,  $y = 1.09x$ ,  $R^2 = 0.99$ ,  $EF = 0.96$ ), and generic mallee eucalypt allometric equations ( $\square$ ,  $y = 0.96x$ ,  $R^2 = 0.99$ ,  $EF = 0.99$ ), and (b) 17 sites which were operationally harvested using generic species-specific allometric equations ( $\bullet$ ,  $y = 0.94x$ ,  $R^2 = 0.92$ ,  $EF = 0.91$ ), and generic mallee eucalypt allometric equations ( $\square$ ,  $y = 0.90x$ ,  $R^2 = 0.90$ ,  $EF = 0.87$ ). Grey dash line is the 1:1 line.

**Table 5**

Verification of allometry-predicted biomass of uncut (non-coppiced) trees across direct measurement sites (site-level analyses where predictions for individual trees within each plot were summed and expressed on a per area basis, and then averaged across plots within a site,  $\text{Mg ha}^{-1}$ ), or across all individual tree biomass datasets collated from a much wider range of sites (individual-level analyses,  $\text{kg individual}^{-1}$ ).  $N$  represents the number of direct-measurement sites in the site-level analyses, or the number of individual trees used in the testing of equations at the individual-level analyses. Bias (expressed as a percentage of observed biomass, % Bias), precision (expressed as a standard deviation of residuals,  $sd(e)$ ), and mean squared error of prediction ( $MSEP$ ) were each calculated on a log-transformed scale. Model efficiency ( $EF$ ) and percentage error in biomass prediction (%  $EBP$ ) were calculated on the back-transformed predictions of above-ground biomass (i.e. original scale). Values in parentheses represent the increase in  $EF$  relative to the most generalised allometry (i.e. generic multi-species equation).

Allometric equation	$N$	% Bias	$sd(e)$	$MSEP$	$EF$	% $EBP$
<i>Between-site; manual whole-plot harvest</i>						
Generic multi-species	6	−0.84	0.087	0.009	0.987	−2.88
Generic species-specific	6	2.37	0.122	0.020	0.959 (−0.03)	7.96
Site-and-species specific	6	0.02	0.001	0.000	1.000 (0.01)	0.08
<i>Between-site; mechanical whole-plot harvest</i>						
Generic multi-species	17	−4.31	0.275	0.093	0.869	−8.87
Generic species-specific	17	−2.23	0.261	0.073	0.916 (0.05)	−6.75
<i>Within-site; tested from individual tree data obtained from 147 sites</i>						
Generic multi-species	2319	−1.48	0.351	0.123	0.867	–
Generic species-specific	2319	−1.16	0.328	0.108	0.889 (0.02)	–
Site-and-species specific	2319	−0.88	0.284	0.081	0.915 (0.05)	–

between  $\pm 16\%$  and  $\pm 21\%$ , and tended to increase with tree size (Fig. 5).

Studying generic equations of trees from mixed-species plantings in Australia, Paul et al. (2013) also showed % $EBP$  was relatively high (i.e. up to 45%) at sites with high biomass ( $>100 \text{ Mg ha}^{-1}$ ). This may be partly attributable to high prediction uncertainty for trees of high stem diameters (see 95% confidence intervals of prediction in Figs. 2–4). This in turn could be attributable to the fact that: (i) there was high variability in biomass observed in large trees, together with the often small-sample number, and (ii) linear allometric equations developed on transformed data may not give due weighting to larger trees which hold a majority of the site biomass. Further work is also required to test the merits of using non-linear allometric equations which provide a higher weighting to larger trees (Brown et al., 1989; Bi and Hamilton, 1998; Parresol, 1999; Ritson and Sochacki, 2003; Bi et al., 2004; Búquez and Martínez-Yrizar, 2011; Morote et al., 2012).

Accuracy of allometry-predicted biomass, as quantified by  $EF$ , was predominantly influenced by precision rather than bias. Further, when applying equations to estimate biomass at a site-level as opposed to making generalisations across a region, precision is particularly important. As shown in Table 5, there was generally lower precision (i.e. higher standard deviation of residuals), and thus accuracy (i.e. lower  $EF$ ), with the application of generic as

opposed to specific equations both at a site-level, and individual-tree level. When tested on either a site-basis or an individual-tree basis, inclusion of site-specific factors in generic equations increased  $EF$  by up to only 0.05. It should be noted that when testing site-and-species-specific allometric equations, the observed and ( $CF$ -adjusted) predicted means should be mathematically identical in each case. This explains the perfect  $R^2$  (Fig. 5) and relatively high  $EF$  values (Table 5) of the site-and-species specific equations.

In terms of testing the precision of generic and specific allometry on an individual tree basis, our findings were consistent with previous work on mixed-species environmental plantings (Paul et al., 2013), woodlands (Williams et al., 2005) eucalypt plantations (Montagu et al., 2005), and secondary forests (van Breugel et al., 2011). These studies also demonstrated there were only minor ( $<0.05$ ) decreases in  $EF$  and/or  $R^2$  when generic rather than site-specific equations were used.

It follows that when estimating biomass at a site-level, site-and-species-specific equations should be applied for highest precision. However when making generalisations of biomass across a region, either multi-species or species-specific generic equations will be suitable as they provide unbiased estimates across a range of sites. An important caution is that tree-based estimates attained from site-and-species specific equations may not necessarily be unbiased if the allometric equation was developed using a small

sample number (e.g. Chave et al., 2004; Paul et al., 2013b). Another important caution is that the generic equations developed have a constrained domain of application. Previous work has shown that when the domain becomes too large (e.g. pan-continental), verification often fails (Madgwick et al., 1991; Basuki et al., 2009; Vieilledent et al. 2012). Here, the domain for young (<16- and <5-years-old uncut and coppiced, respectively) mallee eucalypt trees was regions of southern Australia with 250–850 mm rain year<sup>-1</sup>.

#### 4. Conclusions

Estimates of above-ground biomass made using allometric equations were tested against direct measures for mallee eucalypt plantings in the medium-low rainfall regions of southern Australia. The results showed that when regional- or estate-level estimates of biomass are required, application of generic allometric equations provide percentage errors of biomass prediction of less than  $\pm 9\%$ . However at a given site, and applying the same generic allometrics, these errors could be as high as 16–21%. Given this, together with the finding that precision, and therefore accuracy, tended to decline with increased levels of generality of allometry (e.g. model efficiency decreasing by up to 5%), when making estimates of above-ground biomass at the site-level, site-and-species-specific allometrics provide estimates with the greatest level of accuracy.

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