

Development and testing of allometric equations for estimating above-ground biomass of mixed-species environmental plantings



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ABSTRACT

To quantify the impact that planting indigenous trees and shrubs in mixed communities (environmental plantings) have on net sequestration of carbon and other environmental or commercial benefits, precise and non-biased estimates of biomass are required. Because these plantings consist of several species, estimation of their biomass through allometric relationships is a challenging task. We explored methods to accurately estimate biomass through harvesting 3139 trees and shrubs from 22 plantings, and collating similar datasets from earlier studies, in non-arid (>300 mm rainfall year $^{-1}$) regions of southern and eastern Australia. Site-and-species specific allometric equations were developed, as were three types of generalised, multi-site, allometric equations based on categories of species and growth-habits: (i) species-specific, (ii) genus and growth-habit, and (iii) universal growth-habit irrespective of genus. Biomass was measured at plot level at eight contrasting sites to test the accuracy of prediction of tonnes dry matter of above-ground biomass per hectare using different classes of allometric equations. A finer-scale analysis tested performance of these at an individual-tree level across a wider range of sites. Although the percentage error in prediction could be high at a given site (up to 45%), it was relatively low (<11%) when generalised allometry-predictions of biomass was used to make regional- or estate-level estimates across a range of sites. Precision, and thus accuracy, increased slightly with the level of specificity of allometry. Inclusion of site-specific factors in generic equations increased efficiency of prediction of above-ground biomass by as much as 8%. Site-and-species-specific equations are the most accurate for site-based predictions. Generic allometric equations developed here, particularly the generic species-specific equations, can be confidently applied to provide regional- or estate-level estimates of above-ground biomass and carbon.

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1. Introduction

Afforestation of low productive agricultural land is an opportunity to sequester atmospheric carbon and potentially make a con-

tribution to climate change mitigation (IPCC, 2007). We need to understand rates of carbon sequestration by different types of planted forests (single- or mixed-species, native or exotic species). While there is information on single-species plantations, less is

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known about the potential for native mixed-species plantings, which can provide additional environmental benefits such as enhancing biodiversity (e.g. Bennett and Ford, 1997; Felton et al., 2010) and reclamation from dry-land salinity (e.g. Stirzaker et al., 2002). Accurate and efficient estimation of biomass in such plantings is central to understand and monitor their net contribution for sequestering atmospheric carbon.

In Australia, environmental plantings accounted for up to 20% of the 1.14 Mha of afforestation which has occurred between 1990 and 2012 (DCCEE, 2012). Recent Government policy incentives (e.g. DSEWPAC, 2012) encourage land owners to establish plantings for both natural resource management and sequestration of carbon outcomes (e.g. Harper et al., 2007; Mitchell et al., 2012). Accordingly, an increased rate of establishment of environmental plantings is expected. In order to assess the likely returns for carbon and environmental benefits, and thereby facilitate investment, reliable and accurate estimates of biomass production are required. However, because these plantings are largely established on marginal land, costs associated with current measurement of biomass carbon could be a significant proportion of the carbon credits likely to be obtained (Polglase et al., 2013; Paul et al., 2013a). It is therefore essential that biomass estimates are obtained as efficiently as possible to reduce costs while maintaining accuracy. One way is to develop and apply improved allometric equations (e.g. relationships between stem diameter and live biomass) to convert field inventory data to stand-based estimates of biomass.

Because there may be over 100 species in mixed-species plantings (e.g. Preece et al., 2012), it is impractical to develop species-specific allometric equations for each species at all sites. Efficiency may be improved through the use of generalized equations which are applicable to measurements across sites and species. These should be tested given they may result in some loss of precision (e.g. Williams et al., 2005).

Several studies have developed generic equations for mixed-species plantings in southern Australia (Forrester et al., 2005; Hamilton et al., 2005; England et al., 2006; Barton and Parekh, 2006; Paul et al., 2008, 2010; Hawkins et al., 2010; Hobbs et al., 2010; Jonson and Freudenberger, 2011). These studies have shown that the precision of the generic equations is appropriate for the species and locations in which they were developed, but their reliability for a wider set of species, or locations, remain unknown. There is a need to determine whether generalised equations are applicable broadly, and whether they are best applied constrained within species, genus and growth-habit (i.e. tree or shrub form), or even wider groupings of trees or shrubs.

The objective of this study was to determine the loss in accuracy with increased generality of allometric equations for mixed-species plantings by testing predictions of above-ground biomass against that directly measured by whole-plot harvesting. The impact of including categories of site (namely climate) and species factors on the efficiency of these equations was also assessed.

2. Methods

2.1. Study sites

Several sources of data on individual tree or shrub above-ground biomass were utilised in this study (Table 1). These datasets were collated from sites in southern and eastern Australia (where rainfall was >300 mm year⁻¹, Fig. 1), and were grouped into six categories based on genus and/or growth-habit. Three of these were categories of trees: *Eucalyptus*, *Acacia* and Casuarinaceae (*Allocasuarina* and *Casuarina*) species. There were also three categories of shrubs: *Acacia* and *Melaleuca* species, and other shrubs such as shrub-form species of *Atriplex*, *Bedfordia*, *Dodonaea*, *Cassia*, *Calothamnus*, *Eremophila*, *Gynatrix*, *Hedycarya*, *Leptospermum*, *Olearia*, *Pomaderris*, *Prostanthera*, *Rhagodia*, and *Senna*. These were largely from environmental plantings, some from remnant native woodlands and others from farm forestry plantings.

In addition to collecting data from previous work, we measured above-ground biomass of 3139 individual trees and shrubs from 22 sites, representing contrasting climatic regions and planting types (Table 2). At eight of these sites, whole-plots were harvested and above-ground biomass determined. This was used for assessing the bias, precision and accuracy of different classes of allometric equations in order to validate them. Table 3 provides a summary of characteristics of these eight sites. The key mix of species at each of these sites varied as listed: Strathearn (*E. blakelyi*, *E. camaldulensis*, *E. cinerea*, *E. crenulata*, *E. macarthurii*, *E. mannifera*, *E. melliodora*, *E. polyanthemos*, *E. stellulata*, *E. viminalis*, *A. baileyana*, *A. decurrens*, *A. cardiophylla*, *A. rubida*), Moir (*E. leucoxylon*, *E. loxophleba*, *E. occidentalis*, *E. phaenophylla*, *E. platypus*, *E. pluricaulis*, *E. spathulata*, *E. sporadic*, *E. utilis*, *A. acuminata*, *A. micobotrya*, *A. cyclops*), Jenharwill (*E. leucoxylon*, *A. decurrens*, *A. brachybotrya*, *A. calamifolia*, *A. hakeoides*, *A. pycnantha*), Gumbinnen (*E. fasciculosa*, *E. largiflorens*, *A. pycnantha*, *A. trineura*), Moorland (*E. calycogona*, *E. incrassata*, *E. leptophylla*, *E. phenax*, *E. porosa*, *E. socialis*, *A. calamifolia*, *Melaleuca* sp., *Casuarina* sp.), and Leos (*E. globulus*, *E. kitsoniana*, *E. melliodora*, *E. talyuberup*, *E. tereticornis*, *A. baileyana*, *A. penninervis*, *Melaleuca*

Table 1

Number of individual trees and shrubs included in the collected dataset to represent different species and/or growth-habits, where – indicates no data available.

Trees			Shrubs			Source
<i>Eucalyptus</i>	<i>Acacia</i>	Casuarinaceae	<i>Acacia</i>	<i>Melaleuca</i>	Other	
1965	365	62	462	115	170	This study
41	23	14	30	16	–	Paul et al. (2010)
35	35	–	28	–	–	England et al. (2006)
–	28	9	17	23	–	Hawkins et al. (2010)
316	130	5	69	14	69	G. McArthur pers. com.
–	11	–	–	–	–	R. Sudmeyer pers. com.
–	12	–	–	–	–	Forrester et al. (2005)
3	1	–	–	3	–	B. Rose pers. com.
65	7	10	–	–	–	Jonson and Freudenberger (2011)
145	–	–	–	–	–	Barton and Parekh (2006)
18	–	–	–	–	–	Hamilton et al. (2005)
24	–	–	–	–	–	Paul et al. (2008)
19	–	–	–	–	–	S. Theiveyanathan pers. com.
9	–	–	5	1	–	Hobbs et al. (2010)
2640	612	100	611	172	239	4374 Totals

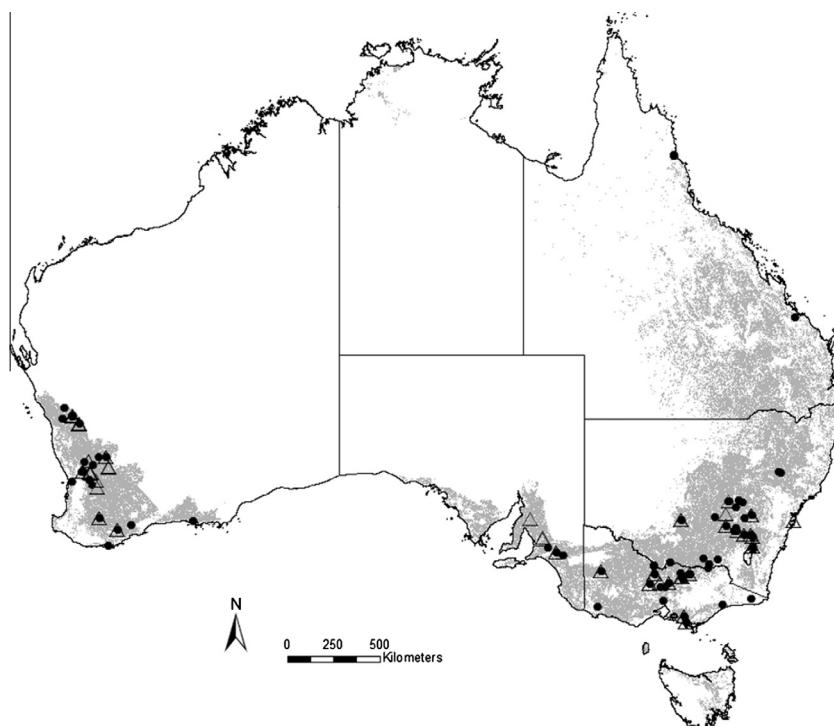


Fig. 1. Location of sites where trees (●) and shrubs (Δ) were sampled for above-ground biomass. Shaded area represents area of Australia where the generic allometric equations are applicable; cleared areas of Australia where mean rainfall is greater than 300 mm year⁻¹.

Table 2

Summary of sites and species: location (in decimal degrees), rainfall, planting type (DS, direct seeded; TS, tube stock; B, broadcast; L, linear planting; B, block planting), number of trees harvested, planting year, and age.

Site	Location	Rain (mm year ⁻¹)	Planting type	Trees/shrubs harvested	Planting year	Age (years)
<i>Direct measurement of biomass (whole-plot harvesting)</i>						
Strathearn	-35.0485, 149.2325	637	DS-B	801	1995	15
Moir	-34.2809, 118.1820	439	DS-B	517	1990	20
Jenharwill	-36.3958, 144.4304	406	TS-L	286	1999	12
Gumbinnen	-36.2447, 141.8148	347	TS/DS-B	178	2001	10
Moorland	-35.3377, 139.6317	370	TS-B	50	1991	20
Moorland	-35.3332, 139.6351	370	TS-B	83	1996	15
McFall 1	-33.7300, 117.3250	438	B-L	111	1990	22
Leos	-37.8381, 147.7582	626	TS-L	93	1996	16
<i>Individual tree or shrub harvesting, and no whole-plot harvesting</i>						
McFall 2	-33.7290, 117.3200	438	B-L	178	1997	15
McFall 3	-33.7320, 117.3147	438	B-L	20	1988	24
Gunbower 1	-35.9800, 144.3847	350	TS-B	40	2002	9
Gunbower 2	-35.9828, 144.3833	350	TS-B	57	2003	8
Lynvale	-37.8987, 141.6380	678	DS-B	80	2003	8
Palomar 1	-33.7972, 145.7389	362	TS-L	6	1993	19
Palomar 2	-33.8032, 145.7451	362	DS-B	94	1998	
Netherleigh	-24.2124, 151.2977	884	TS-B	191	2002	9
Batters 1	-38.6675, 145.9887	869	B-L	109	2001	11
Batters 2	-38.6686, 145.9925	869	B-L	21	2000	12
Batters 3	-38.6715, 145.9895	869	B-L	24	2003	9
Suttons	-38.3998, 145.8996	1050	TS-B	88	2004	8
Shannonvale	-16.5050, 145.3766	2075	TS-B	39	1992–93	19–20
Julatten	-16.559, 145.358	1475	TS-B	73	1992–93	19–20
				3139		
						Totals

sp.). For each site, the equation applied to each individual tree or shrub was dependent on the species.

2.2. Above-ground biomass sampling

For species at each site listed in Table 2, individuals representing a range of stem sizes were randomly selected for measurement of above-ground biomass. A minimum of 10 individuals were

sampled for each species planted at most sites. At some sites where individual trees or shrubs were harvested (i.e. sites which were not direct measurement sites) there were insufficient numbers of trees present to increase the sample number above 10. At the direct-measurement sites indicated in Table 2 and characterised further in Table 3, all trees and shrubs were harvested and weighed.

Using a diameter measuring tape, stem diameters were measured on all trees and shrubs. The height at which diameters were

Table 3

Summary of the plantings where direct measurements of biomass were made, including plot size (ha) and number plots, number of individual trees or shrubs harvested (individuals harvested), stand density (trees per hectare), stand basal area (BA, using a DBH equivalent estimate for all individuals within the plots), and the measured above-ground biomass (AGB, Mg ha⁻¹).

	Size (ha)	Plots	Plot size (ha)	Stand density (trees ha ⁻¹)	BA (m ² ha ⁻¹)	AGB (Mg ha ⁻¹)
Strathearn	4.30	12	0.48	2827	11.37	38.9
Moir	5.05	12	0.48	2708	4.72	42.4
Jenharwill	1.52	6	0.05	6456	16.92	69.1
Gumbinnen	18.4	6	0.22	2282	4.38	19.1
Moorlands 1	2.76	4	0.36	139	2.52	20.0
Moorlands 2	1.99	4	0.36	244	2.88	18.6
McFall 1990	1.46	3	0.36	2440	30.50	189.6
Leos	1.67	10	0.11	845	26.61	113.6

measured varied between sites based on the heights of the trees/shrub and the average height at which they forked or branched. Where required, relationships between stem diameters at different heights were converted to diameters measured at 130 cm height (DBH) for trees, or 10 cm height (D10) for shrubs. For each growth-habit, a linear relationship between stem diameters at DBH (or D10) and another diameter measured on the same tree (or shrub) at a differing height were established (average $R^2 = 0.94$ and $N = 484$). For analysis, we combined the diameters for each stem of multi-stemmed individuals (D_i) to a single value (equivalent single diameter, $D_e = \sqrt{\sum D_i^2}$) so that the total basal area for all stems was equal to the basal area of a tree with this equivalent single diameter.

Three to five representative individuals of each species at each site were sampled for moisture content. Each tree was divided into: (i) live crown (all foliage and twigs <40 mm in diameter), and (ii) the remaining stem and branches. The fresh weights of these were measured in the field. Sub-samples (three replicates, ca. 2–3 kg) of each component were weighed and oven-dried at 70 °C to a constant weight. On a tree-by-tree basis, moisture contents were calculated for each component and used to calculate the dry weight. For shrubs, moisture measurements were made on a whole-above-ground plant basis.

2.3. Development of allometric equations for above-ground biomass

Four types of allometric equations were developed: (i) site-and-species-specific, (ii) generic species, or species-specific but applicable across sites, (iii) generic growth-habit based, and (iv) generic universal, including all trees and shrubs for all genera and species. Growth-habit was grouped into different genera of trees and shrubs on the basis of either statistically-different allometry, and/or unique form (of tree growth-habit typically indicated by >5 tall stems, or shrub growth-habit typically indicated by >5 short stems).

For each equation, 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, kg tree⁻¹, expressed on a dry-weight basis), x is the independent variable (stem diameter, cm), a' is the intercept, b is the scaling allometric exponent, and e' is the error term. Parameters a' and b were estimated using linear least-squares. For generic growth-habit and generic universal equations trees <1 cm stem diameter and/or <1 kg tree⁻¹ were excluded because they contributed relatively little to biomass and caused high residual variance. The 95% confidence intervals of both the regression, and the prediction interval,

were calculated for each equation developed (e.g. Picard et al., 2012).

The logarithmic transformation to linearise the power function also corrected heteroscedasticity. Because logarithmic regressions produce biased estimates of biomass following back-transformation from logarithm, bias corrections were calculated using the ratio of arithmetic sample mean and mean of the back-transformed predicted values from the regression as described by Snowdon (1991).

2.4. Statistical analysis of allometric equations

When fitting allometric equations, unequal numbers of observations among sites might 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). Possible impacts of unequal numbers of observations among sites on parameters a' and b were therefore explored. Least sum squares of residuals were solved using a weighting applied to the residuals based on the number of observations per site. 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. For the range of stem diameters and species across which biomass datasets were collated, allometry-predictions of biomass were made using parameters a' and b resulting from this site-weighting approach. Resulting predictions of biomass were then compared to those obtained without weighting.

A key challenge in the development of generic growth-habit allometric equations was to determine the most appropriate categorisation of different growth-habits. It was considered that there were at least six possible categories: (i) *Eucalyptus* trees, but with this category also including some other tree-form species, such as *Corymbia* and *Codonocarpus* species (2% of this category), and tree-form genera from in tropical regions of eastern Australia (14% of this category) such as *Alstonia*, *Araucaria*, *Blepharocarya*, *Elaeocarpus*, *Flindersia*, *Melicope*, *Xanthostemon* species, (ii) *Acacia* trees largely from temperate regions, with some (8%) from tropical regions of eastern Australia, (iii) Casuarinaceae trees, (iv) *Acacia* shrubs, (v) *Melaleuca* shrubs, and (vi) other temperate region shrubs (*Callitris*, *Cassia*, *Dodonaea*, *Atriplex*, *Calothamnus*, *Leptospermum*, *Pomaderris*, *Prostanthera*, *Olearia*, *Bedfordia*, *Gynatrix*).

An ANCOVA analysis facilitated the assessment of appropriate groupings of these growth-habits based on the assessment of significant differences in slope and/or intercepts between the log-transformed explanatory variable of stem diameter and log-transformed biomass for following factors: (i) generic universal groupings: factor levels being trees (groups i, ii and iii), tall shrubs (groups iv) and small shrubs (groups v and vi), and (ii) growth-habit groupings: factor levels being *Eucalyptus*, *Acacia* and Casuarinaceae sp. for tree growth-habits, and *Melaleuca* sp. and other shrubs for small shrub growth-habits. Levene's test was used to confirm homogeneity of variances across categories, and where significant differences were detected ($\alpha = 0.05$), Tukey's test was used to determine the least significant difference among categories.

It has been suggested that trees growing in tropical regions tend to have lower wood densities and different growth forms compared to those in temperate regions (e.g. Keith et al., 2009; Stegen et al., 2011), raising the question of whether generic growth-habit equations could be based on climate (tropical versus temperate regions, or high versus low rainfall). This was tested, using ANCOVA analysis, for the larger categories of *Eucalyptus* trees and *Acacia* trees ($N = 612$ –2387 from over 69–115 sites). Levene and Tukey tests were applied as described above. The climate factors in this analysis were: (i) low-rainfall temperate, (ii) high-rainfall temperate and (iii) tropical. Tropical regions in Australia were defined as having hot (or warm) humid summers as per the temperature

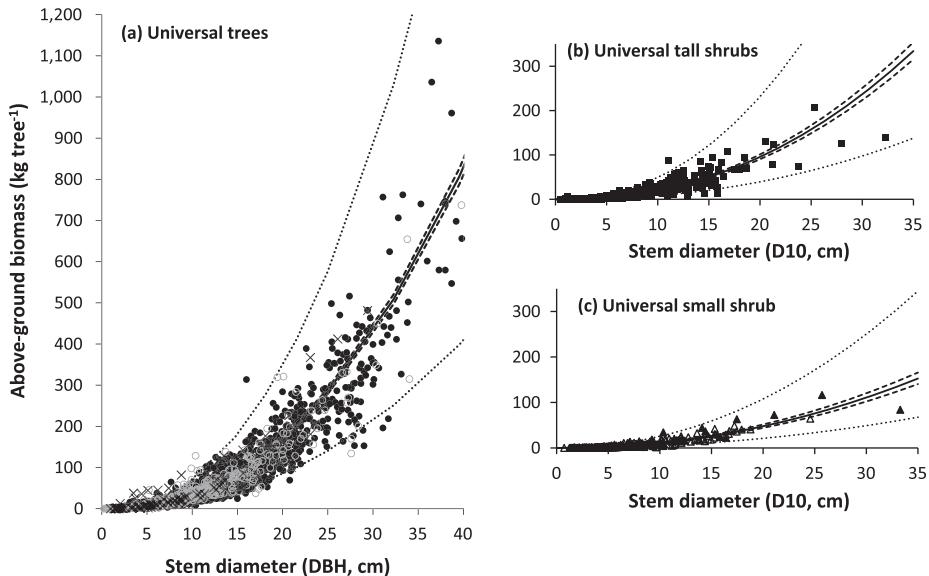


Fig. 2. Generic universal allometric equations for above-ground biomass of: (a) trees, (b) tall shrubs, and (c) small shrubs found in environmental plantings. The generic universal relationships for trees include trees of species of: *Eucalyptus* (●), *Acacia* (○), and *Casuarinaceae* (×). The universal relationship for tall shrubs include *Acacia* shrub species. The generic universal relationship for small shrubs include shrubs species of: *Melaleuca* (Δ), and other shrubs (▲). Parameters for these fitted equations are provided in Table 4. Dotted and dashed lines represent the 95% confidence interval of the regression, and the 95% prediction interval, respectively. Plot for trees in (a) includes only trees with stem diameters <40 cm (2% of the dataset exceptionally larger trees not shown). Note, allometric equations were fitted on transformed scale, but untransformed data are presented here.

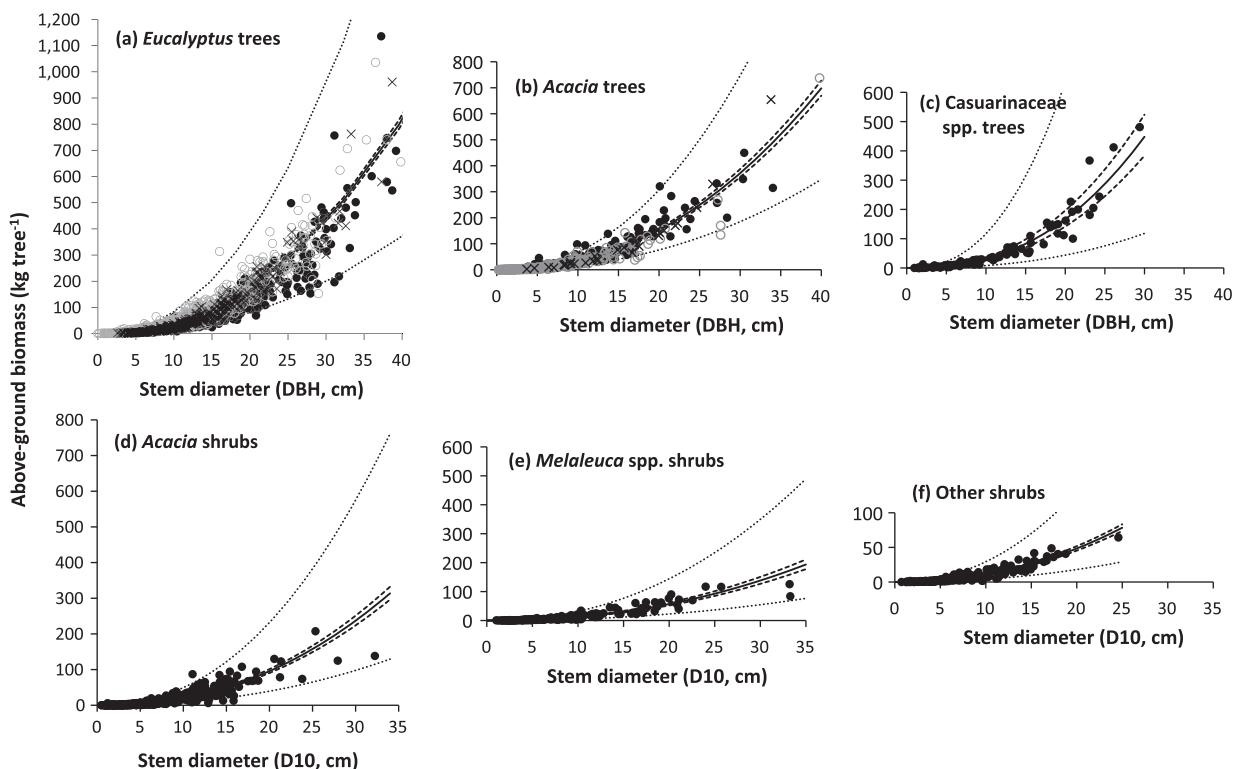


Fig. 3. Allometric equations for above-ground biomass of the key genera/growth-habits found in environmental plantings, including: (a) *Eucalyptus* (namely) tree species, (b) *Acacia* tree species, (c) *Casuarinaceae* tree species, (d) *Acacia* shrub species, (e) *Melaleuca* shrub species, and (f) other shrubs. Plots (a) and (b) show data points from tropical regions (×), and temperate regions of low and high rainfall, defined as having a MAR of <500 (○) or >500 mm (●). Parameters for fitted equations are provided in Table 4. Dotted and dashed lines represent the 95% confidence interval of the regression, and the 95% prediction interval, respectively. Plot for trees in (a) includes only trees with stem diameters <40 cm (2% of the dataset exceptionally larger trees not shown). Note, allometric equations were fitted on a log-transformed scale, but untransformed data are presented here.

humidity zones of the BOM (2006) climate classification. Low rainfall regions were defined as 300–500 mm year⁻¹, thereby resulting in two categories of rainfall with approximately equal-sized datasets. A categorical rather than empirical analysis of climate or rain-

fall were used as one of the planned applications of this work was to utilise these equations for calibration of forest growth and carbon accounting models requiring parameters based on planting categories.

Table 4

Summary of values of the parameters a and b in generic allometric equations for above-ground biomass, and the number of sites from which biomass data were derived (sites), sample number (N , number of individuals used to develop the allometric equation), Snowdon (1991) correction factor (CF), and model efficiency (EF, Soares et al. 1995), and precision (expressed as a standard deviation, $sd(e)$). All equations fitted were highly significant ($P < 0.001$). Values in parenthesis are the stem diameters below which the equation may be applied. Trees include species of *Eucalyptus*, *Acacia*, and Casuarinaceae, tall shrubs include species of *Acacia* shrub, while small shrubs include *Melaleuca* and other species.

Species	Explanatory variable	Sites	N	a	b	CF	EF	$sd(e)$
<i>Generic universal allometric equations</i>								
Tree (<100 cm)	DBH	148	3352	-1.82	2.27	1.18	0.91	0.359
Tall shrub (<30 cm)	D10	39	611	-2.23	2.24	1.08	0.85	0.449
Small shrub (<35 cm)	D10	51	411	-2.45	2.08	1.09	0.83	0.410
<i>Generic growth-habit allometric equations</i>								
Generic <i>Eucalyptus</i> tree (<100)	DBH	115	2640	-1.71	2.21	1.29	0.93	0.360
Generic <i>Acacia</i> tree (<40 cm)	DBH	69	612	-1.59	2.19	1.05	0.93	0.354
Casuarinaceae sp. (<30 cm)	DBH	18	100	-2.22	2.45	1.01	0.91	0.662
Generic <i>Acacia</i> shrub (<30 cm)	D10	39	611	-2.23	2.24	1.08	0.85	0.449
<i>Melaleuca</i> sp. (<35 cm)	D10	29	172	-2.57	2.19	1.06	0.91	0.465
Shrub sp. (<25 cm)	D10	22	239	-2.68	2.16	1.09	0.87	0.499

The software used for ANCOVA analyses, Levene and Tukey tests was R-Stats version 2.15.2.

2.5. Validation of biomass predictions: bias, precision and accuracy

Bias and precision, as well as overall accuracy of allometry-predicted biomass, were quantified by analysis of the residuals (e_i):

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

where E_i is the equation-predicted biomass of the observation i , and O_i is the measured biomass of the same observation. 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:

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

where \bar{e} is the mean of n residuals and quantifies the bias, and $var(e)$ 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 ($sd(e)$). The %Bias, $sd(e)$ and $MSEP$ were all calculated on the log-transformed scale.

Another quantity which was used to assess accuracy and the overall fit of the equation was model efficiency index (EF, Soares et al., 1995), defined as:

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

where \bar{o}^2 is the mean square deviation of each observation from the mean 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 (generic universal, generic growth-habit, generic species specific and site-and-species specific), %Bias, $sd(e)$, $MSEP$ and EF were calculated by comparing predictions with biomass observed at two scales; site-level (where predictions for individual trees and shrubs within each plot were summed and expressed on a per area basis, and then average across plots within a site), and individual-tree or shrub level (where individual tree or shrub biomass predictions were available from a large number of sites). The primary analysis was at the site-level, whereby the equations are used to predict whole-plot biomass, which are then compared to the actual harvested biomass of the same plots. This analysis provides a direct test of the overall applicability of the allometrics across a broad range of sites. For each class of equation, the percentage error in

biomass prediction (%EBP) was calculated from the average percentage difference between predicted and observed site biomass (in $Mg\ ha^{-1}$) across the eight direct measurement sites. The individual-scale analysis of bias, precision and accuracy utilised all biomass datasets collated (Table 1, although excluding Casuarinaceae, *Melaleuca* and other shrub species from the species-specific equation tests because species names were not documented), and entailed a comparison of biomass of individuals with its predicted value estimated from the four different classes of equations. It thereby provided a more detailed assessment of the variability between the four classes of equations in terms of performance across a much wider range of sites. Datasets were excluded when $N < 6$ for any given species-by-site combination (comprising 8% of combinations).

3. Results and discussion

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

The four classes of equations for prediction of above-ground biomass are presented in various forms. For the two most generalised equations (both generic universal models and generic growth-habit based models) figures are provided (Figs. 2 and 3, respectively). Parameters for these, and stem diameter ranges over which they are applicable, are given in Table 4. For the species-specific (generic and site-specific) equations, the number of equations were too numerous to represent in figures. Parameters for the generic species-specific equations, and stem diameter ranges over which they are applicable, are provided in Table 5. Because site-and-species specific equations have less reliability outside the sites for which the data was obtained, the parameters for these equations are not listed. Instead, the site-and-species specific equations for the eight sites where biomass was directly determined are shown in Fig. 4.

As observed by others (e.g. Bi et al., 2010), uncertainty in prediction of biomass was large for a given tree or shrub, particularly for large trees or shrubs where observations were few (Figs. 2 and 3). This was the case for all equations. Results in Fig. 4 show that site-and-species specific equations were generally within the 95% confidence interval of prediction from generic growth-habit equations. There was little evidence in the directly measured data that predicted biomass from the various species-specific equations result in consistently higher or lower estimates than that derived from more generalised equations. The only exception was the data from the Leos site where many of the species-specific equations

Table 5

Summary of values of the parameters a' and b in species-specific allometric equations for above-ground biomass, number of sites from which biomass data were derived (sites), sample number (N , number of individuals used to develop the allometric equation), Snowdon (1991) correction factor (CF), model efficiency (EF , Soares et al. 1995), and precision (expressed as a standard deviation, $sd(e)$). All equations fitted were highly significant ($P < 0.001$). Values in parenthesis are the stem diameters below which the equation may be applied.

Species	Sites	N	a	b	CF	EF	$sd(e)$
<i>Eucalyptus</i> trees (using DBH as the explanatory variable)							
<i>Alstonia scholaris</i> (for <12 cm)	1	6	-1.29	2.11	1.00	0.916	0.103
<i>Araucaria cunninghamii</i> (for <25 cm)	1	6	-1.75	2.29	1.00	0.979	0.117
<i>Blepharocarya involucrigera</i> (for <40 cm)	1	14	-1.50	2.16	1.01	0.964	0.123
<i>Codonocarpus cotinifolius</i> (for <16 cm)	5	17	-1.17	1.91	1.03	0.722	0.308
<i>Corymbia intermedia</i> (for <17 cm)	1	13	-2.14	2.19	1.03	0.966	0.203
<i>C. maculata</i> (for <60 cm)	6	37	-1.79	2.33	1.07	0.990	0.165
<i>C. tessellaris</i> (for <13 cm)	1	22	-2.40	2.35	1.03	0.956	0.202
<i>Eucalyptus albida</i> (for <15 cm)	1	18	-1.10	2.15	1.02	0.964	0.154
<i>E. annulata</i> (for <30 cm)	2	10	-1.76	2.36	0.96	0.984	0.215
<i>E. argophloia</i> (for <15 cm)	1	25	-1.11	2.03	1.01	0.906	0.163
<i>E. argyaphaea</i> (for <28 cm)	2	7	-1.09	2.02	0.91	0.992	0.119
<i>E. astringens</i> (for <30 cm)	2	16	-1.62	2.26	0.97	0.954	0.326
<i>E. blakelyi</i> (for <20 cm)	8	47	-1.84	2.15	1.08	0.966	0.323
<i>E. bridgesiana</i> (for <20 cm)	8	17	-1.35	1.93	1.06	0.953	0.335
<i>E. calycogona</i> (for <25 cm)	1	7	-1.11	2.12	1.02	0.845	0.263
<i>E. camaldulensis</i> (for <70 cm)	8	89	-1.67	2.19	1.42	0.955	0.224
<i>E. captiosa</i> (for <20 cm)	3	7	-0.97	2.06	1.05	0.974	0.231
<i>E. cinerea</i> (for <30 cm)	1	27	-1.21	1.83	1.15	0.868	0.513
<i>E. cladocalyx</i> (for <55 cm)	4	37	-1.36	2.30	1.13	0.979	0.291
<i>E. cloeziana</i> (for <40 cm)	2	10	-4.26	3.06	0.13	0.990	0.119
<i>E. crebra</i> (for <15 cm)	1	15	-2.03	2.27	1.03	0.946	0.227
<i>E. crenulata</i> (for <20 cm)	1	10	-1.97	2.35	1.08	0.952	0.274
<i>E. falcata</i> (for <35 cm)	5	16	-1.20	2.15	1.02	0.985	0.221
<i>E. fasciculosa</i> (for <16 cm)	2	8	-1.41	1.99	1.08	0.834	0.341
<i>E. flocktoniae</i> (for <30 cm)	1	6	-1.56	2.30	1.00	0.982	0.148
<i>E. gardneri</i> (for <32 cm)	2	24	-1.79	2.39	1.00	0.986	0.211
<i>E. globulus</i> (for <39 cm)	3	17	-1.66	2.19	1.01	0.963	0.285
<i>E. horistes</i> (for <12 cm)	6	22	-0.70	1.78	1.01	0.877	0.284
<i>E. incrassata</i> (for <20 cm)	1	10	-1.72	2.31	1.06	0.825	0.359
<i>E. kitsoniana</i> (for <31 cm)	2	34	-1.54	2.11	1.00	0.977	0.247
<i>E. kochii</i> (for <16 cm)	1	17	-1.86	2.31	1.03	0.976	0.173
<i>E. largiflora</i> (for <20 cm)	2	57	-1.23	2.01	1.02	0.943	0.213
<i>E. leptophylla</i> (for <20 cm)	2	11	-2.01	2.37	1.03	0.899	0.361
<i>E. leucoxylon</i> (for <25 cm)	4	28	-1.37	2.07	1.04	0.979	0.140
<i>E. loxophleba</i> (for <30 cm)	42	317	-0.77	1.68	1.31	0.797	0.396
<i>E. macarthurii</i> (for <30 cm)	1	23	-2.08	2.26	1.02	0.937	0.339
<i>E. mannifera</i> (for <25 cm)	1	19	-2.46	2.45	1.04	0.968	0.175
<i>E. melanophloia</i> (for <13 cm)	1	14	-2.83	2.50	1.07	0.929	0.310
<i>E. melliodora</i> (for <39 cm)	7	169	-1.73	2.12	1.17	0.939	0.279
<i>E. microcarpa</i> (for <110 cm)	5	30	-1.92	2.36	1.17	0.983	0.376
<i>E. moluccana</i> (for <27 cm)	1	26	-1.68	2.32	1.01	0.967	0.143
<i>E. obliqua</i> (for <28 cm)	1	14	-2.16	2.23	1.00	0.954	0.259
<i>E. occidentalis</i> (for <80 cm)	6	118	-2.12	2.43	1.18	0.979	0.198
<i>E. ovata</i> (for <30 cm)	2	24	-2.16	2.35	0.99	0.988	0.171
<i>E. phaenophylla</i> (<15 cm)	1	7	0.32	1.38	1.01	0.974	0.117
<i>E. phenax</i> (for <15 cm)	1	7	-2.63	2.65	1.01	0.966	0.193
<i>E. platypus</i> (for <30 cm)	3	39	-0.74	1.98	1.06	0.935	0.288
<i>E. pluricaulis</i> (for <10 cm)	1	9	-1.24	2.24	1.03	0.937	0.284
<i>E. polyanthemos</i> (for <25 cm)	5	51	-1.46	2.05	1.07	0.961	0.264
<i>E. porosa</i> (for <30 cm)	2	33	-1.95	2.30	1.06	0.963	0.201
<i>E. sargentii</i> (for <40 cm)	1	25	-1.66	2.27	1.01	0.951	0.257
<i>E. socialis</i> (for <30 cm)	2	10	-1.73	2.28	1.03	0.867	0.349
<i>E. spathulata</i> (for <45 cm)	1	206	-1.30	2.22	1.00	0.954	0.248
<i>E. sporadica</i> (for <30 cm)	1	11	-1.19	2.10	0.97	0.918	0.346
<i>E. stellulata</i> (for <15 cm)	1	37	-1.63	2.04	1.02	0.951	0.154
<i>E. talyuberlup</i> (for <35 cm)	1	6	-1.36	2.17	1.00	0.984	0.094
<i>E. tereticornis</i> (for <50 cm)	3	71	-2.15	2.34	0.97	0.959	0.347
<i>E. tri-sideroxylon</i> (for <60 cm)	6	54	-2.39	2.40	1.10	0.954	0.125
<i>E. utilis</i> (for <15 cm)	1	18	-0.49	1.85	1.14	0.679	0.626
<i>E. viminalis</i> (for <30 cm)	4	365	-2.19	2.30	1.05	0.954	0.154
<i>E. wandoo</i> (for <22 cm)	3	58	-1.63	2.13	1.27	0.927	0.266
<i>Elaeocarpus angustifolius</i> for (<35 cm)	2	24	-2.17	2.37	1.03	0.958	0.156
<i>Flindersia brayleyana</i> (for <35 cm)	2	19	-1.75	2.29	1.00	0.956	0.145
<i>Lophostemon sauvageolens</i> (for <17 cm)	1	14	-1.78	2.04	1.02	0.951	0.173
<i>Melicope elleryana</i> (for <16 cm)	2	5	-0.81	1.82	1.00	0.977	0.110
<i>Xanthostemon chrysanthus</i> (for <25 cm)	1	5	-3.15	2.82	0.99	0.973	0.179
<i>Acacia</i> trees (using DBH as the explanatory variable)							
<i>A. acuminata</i> (for <30 cm)	35	125	-1.30	1.90	1.17	0.906	0.273
<i>A. baileyana</i> (for <28 cm)	2	44	-0.98	2.05	0.97	0.893	0.236

(continued on next page)

Table 5 (continued)

Species	Sites	N	a	b	CF	EF	sd(e)
<i>A. dealbata</i> (for <31 cm)	5	17	-1.21	2.11	1.06	0.968	0.361
<i>A. decurrens</i> (for <25 cm)	6	36	-1.94	2.43	1.04	0.945	0.279
<i>A. disparrima</i> (for <25 cm)	1	22	-1.99	2.30	1.03	0.974	0.185
<i>A. implexa</i> (for <15 cm)	1	5	-1.53	2.13	1.03	0.990	0.182
<i>A. mangium</i> (for <34 cm)	2	9	-2.28	2.44	1.06	0.989	0.192
<i>A. mearnsii</i> (for <25 cm)	6	48	-2.02	2.46	0.95	0.967	0.157
<i>A. melanoxylon</i> (for <25 cm)	4	51	-1.70	2.15	1.02	0.977	0.253
<i>A. micobotrya</i> (for <25 cm)	1	33	-1.55	2.13	1.07	0.977	0.292
<i>A. murrayana</i> (for <20 cm)	13	15	-1.03	1.85	1.10	0.916	0.300
<i>A. penninervis</i> (for <35 cm)	1	22	-1.00	2.02	0.95	0.952	0.295
<i>A. pycnantha</i> (for <15 cm)	6	33	-1.90	2.33	0.99	0.974	0.204
<i>A. salicina</i> (for <15 cm)	1	13	-1.78	2.16	1.01	0.959	0.208
<i>A. saligna</i> (for <45 cm)	6	50	-2.23	2.42	0.94	0.954	0.279
<i>A. stenophylla</i> (for <15 cm)	1	16	-2.22	2.47	0.99	0.936	0.240
<i>Acacia</i> shrubs (using D10 as the explanatory variable)							
<i>A. brachybotrya</i> (for <15 cm)	1	8	-2.19	2.27	1.03	0.962	0.385
<i>A. calamifolia</i> (for <20 cm)	2	128	-2.23	2.41	1.02	0.939	0.347
<i>A. cardiophylla</i> (for <15 cm)	1	11	-2.11	2.26	1.15	0.773	0.440
<i>A. cyclops</i> (for <20 cm)	1	8	-1.44	2.01	1.06	0.851	0.354
<i>A. deanei</i> (for <35 cm)	5	26	-2.04	2.20	0.97	0.914	0.498
<i>A. hakeoides</i> (for <25 cm)	3	113	-2.10	2.10	1.10	0.946	0.343
<i>A. hemiteles</i> (for <8 cm)	14	49	-3.40	2.39	1.11	0.902	0.427
<i>A. lasiocalyx</i> (for <5 cm)	1	5	-3.33	2.70	0.97	0.977	0.187
<i>A. pendula</i> (for <30 cm)	2	18	-2.91	2.58	1.06	0.985	0.214
<i>A. pycnantha</i> (for <25 cm)	8	102	-2.37	2.36	1.05	0.927	0.262
<i>A. rigens</i> (for <15 cm)	2	22	-2.68	2.41	1.02	0.973	0.174
<i>A. rubida</i> (for <25 cm)	2	18	-2.01	1.95	1.11	0.812	0.492
<i>A. trineura</i> (for <15 cm)	1	48	-1.74	1.84	1.15	0.699	0.790
<i>A. verniciflua</i> (for <15 cm)	3	12	-2.66	2.48	1.07	0.941	0.435
<i>A. victoriae</i> (for <15 cm)	7	21	-4.37	2.93	0.96	0.966	0.252

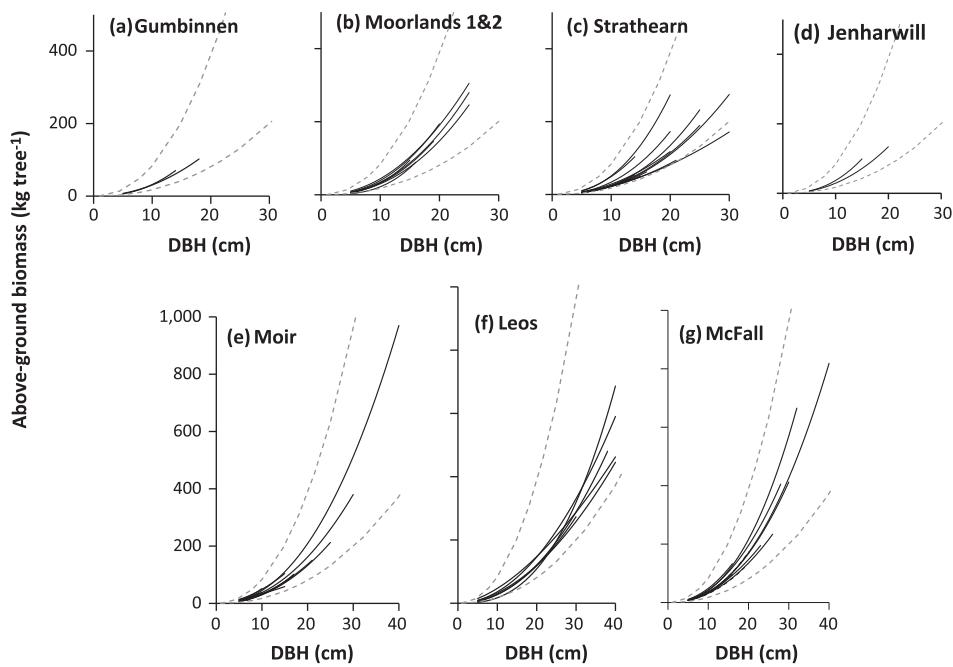


Fig. 4. Example of site-and-species specific allometric equations (black solid lines) for each of the eight direct measurement sites, with only eucalypt tree species shown here, and only for the diameter range for which data were available. Grey dash lines represent the 95% prediction interval of the eucalypt generic growth-habit allometric equation shown in Fig. 3a.

appeared to underestimate biomass when compared to the generic growth-habit equation.

As expected, site-and-species-specific equations had the highest EF of all four classes of equations, with average EF decreasing (with increasing sample size and increasing percentage coefficient of variation) as the generality of the allometry increased. Across all

equations, EF averaged 0.95, 0.94, 0.90, and 0.86 for site-and-species-specific (data not shown), generic species-specific (Table 5), generic growth-habit (Table 4), and generic universal equations (Table 4), respectively.

The fact that EF values for these equations were so high supports the finding from other studies that stem diameter is an

Table 6

ANCOVA results for comparison of allometry between various groupings of the above-ground biomass datasets. Where there were no statistically significant differences in slope, differences in intercepts were tested.

		DF	SS	MS	F	P-value
<i>Comparison between universal grouping of trees, tall shrubs and small shrubs</i>						
Slope	Diameter	1	7739	7739	7733	<0.001
	Group	2	65	32	32.4	<0.001
	Diameter × Group	2	17	9	8.7	<0.001
	Residuals	3959	3962	1		
<i>Comparison between Eucalypts, Acacia trees and Casuarinaceae sp.</i>						
Slope	Diameter	1	6336	6336	6330	<0.001
	Group	2	4	2	1.96	0.14
	Diameter × Group	2	1	1	0.71	0.49
	Residuals	3211	3214	1		
Intercepts	Diameter	1	6336	6336	6332	<0.001
	Group	2	4	2	1.96	0.14
	Residuals	3213	3215	1		
<i>Comparison between Melaleuca sp. and other shrubs</i>						
Slope	Diameter	1	204	204	1210	<0.001
	Group	1	0.50	0.50	2.97	0.09
	Diameter × Group	1	0.04	0.04	0.25	0.62
	Residuals	245	41.2	0.17		
Intercepts	Diameter	1	204	204	1215	<0.001
	Group	1	0.50	0.50	2.98	0.09
	Residuals	246	41.3	0.17		
<i>Comparison between low rainfall, high rainfall and tropical for Eucalypts</i>						
Slope	Diameter	1	5241	5241	5235	<0.001
	Group	2	70	35	35.0	<0.001
	Diameter × Group	2	16	8	7.77	<0.001
	Residuals	2575	2578	1		
<i>Comparison between low rainfall, high rainfall and tropical for Acacia shrubs</i>						
Slope	Diameter	1	179	175		<0.001
	Group	2	1.0	0.52		0.60
	Diameter × Group	2	0.0	0.02		0.98
	Residuals	524	527			
Intercepts	Diameter	1	176	176		<0.001
	Group	2	1.0	0.52		0.60
	Residuals	526	527			

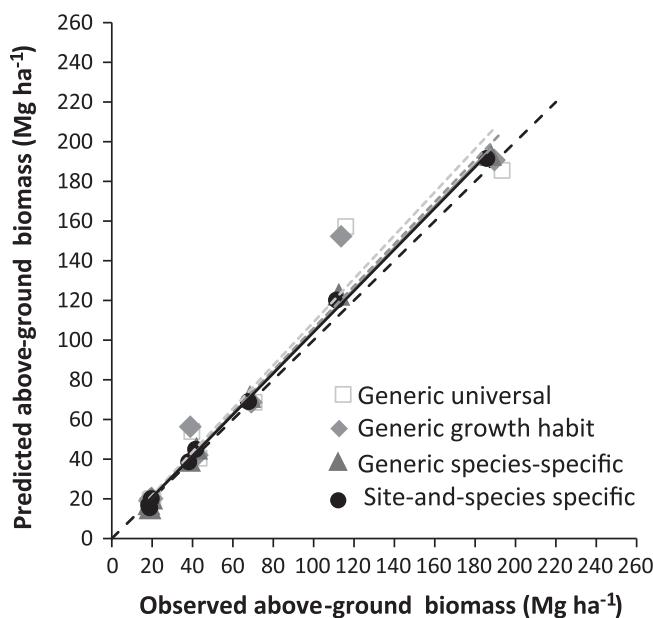


Fig. 5. For each of the four classes of allometry, relationship between predicted and observed above-ground biomass across the eight direct measurement sites (see Table 2). Dashed line indicates the 1:1 line. The best fits (when forced through the origin) for generic universal, generic growth habit, generic species-specific and site-and-species specific relationships gave slopes (and R²'s) of 1.06 (0.94), 1.09 (0.96), 1.05 (1.00) and 1.04 (1.00), respectively.

appropriate predictor of above-ground biomass at site or regional scales, and height or wood density provide relatively little

improvement to the efficiency of predictions (e.g. Brown et al., 1989; Lambert et al., 2005; Paul et al., 2008; Basuki et al., 2009; Xiang et al., 2011). The high EF values also provide further evidence that the simple power-law model has applicability across a wide range of woody species given they have their origins in common geometric, biomechanical 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). However, there is evidence that these power-law models fail for trees larger than those studied here. This may be because of insufficient data to adequately represent large trees. Over-estimates of biomass is common when DBH >50 cm due to accelerated damage and senescence as trees mature (Niklas, 1995; Chambers et al., 2001; Chave et al., 2005; Fatemi et al., 2011).

There appears to be little evidence that species-specific generic equations were influenced by site within which data were pooled. A linear regression analysis between biomass predicted using equations fitted using the site-based weighting and no weighing approach showed little difference between these predictions. When studying individual tree predictions of above-ground biomass from all three classes of generic equations ($N = 9865$), a comparison of results from weighted with un-weighted fitting approaches gave a slope of 1.04 (when forced through the origin), and R² value of 100%. This suggested that pooling of datasets from across multiple sites to develop generic allometric equations was valid.

Assessment was also required for the validity of grouping species into categories for the more generalised equations. For all trees and shrubs, when allometry was compared using the common explanatory variable of D10, there were significant ($P < 0.001$) differences in both the slopes and intercepts among the six possible

Table 7

Verification of allometry-predicted biomass across direct measurement sites (site-level analyses where predictions for individual trees and shrubs within each plot were summed and expressed on a per area basis, and then average across plots within a site, Mg ha⁻¹), or across all individual tree and shrub biomass datasets collated from a much wider range of sites (individual-level analyses, kg individual⁻¹). 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 universal allometric equation). *N* represents the number of direct-measurement sites in the site-level analyses, or the number of individual trees and shrubs used in the testing of equations at the individual-level analyses.

Species	<i>N</i>	%Bias	<i>sd(e)</i>	<i>MSEP</i>	<i>EF</i>	% <i>EBP</i>
<i>Site-level</i>						
Generic universal	8	2.035	0.144	0.027	0.92	9.58
Generic growth-habit	8	2.351	0.141	0.028	0.93 (+0.01)	10.8
Generic species-specific	8	-0.396	0.088	0.008	0.99 (+0.07)	0.07
Site-and-species specific	8	-0.923	0.084	0.008	1.00 (+0.08)	-1.90
<i>Individual tree or shrub level</i>						
Generic universal	3593	-1.847	0.403	0.163	0.92	-
Generic growth-habit	3593	-0.865	0.400	0.161	0.90 (-0.02)	-
Generic species specific	3176	-0.755	0.310	0.096	0.96 (+0.04)	-
Site-and-species specific	3176	-0.221	0.277	0.077	0.99 (+0.07)	-

categories of growth-habits, but with the Tukey test showing main differences were only significant between trees (*Eucalyptus*, *Acacia* and *Casuarinaceae*), tall shrubs (*Acacia* shrub) and small shrubs (*Melaleuca* and other shrubs) (Fig. 2; Table 6). There were no significant differences in allometry among tree growth-habits (i.e. between species of *Eucalyptus*, *Acacia* and *Casuarinaceae*) or among small shrub growth-habits (i.e. between *Melaleuca* and other shrubs species) (Table 6). Inclusion of growth-habit categories within a multiple-regression model for trees or shrubs increased the amount of explained variation in above-ground biomass by <0.01 units (data not shown). Hence, consistent with previous results (Keith et al., 2000; Bi et al., 2004; Jonson and Freudenberg, 2011), we found little evidence of variation in allometry among species within tree growth-habits, or within shrub growth habits. We conclude that key differences in allometry are between trees, tall shrubs and short shrubs. This may be attributed to differences in stem geometry between trees and shrubs related to differences in life-span, wood density and environmental conditions which determine the proportion of branches (e.g. Keith et al., 2000).

Similarly, results supported the lumping of biomass data from different climates within generic equations. For acacia trees, the slopes and intercepts of equations were not significantly different ($P > 0.05$) between the tropical, high rainfall temperate and low rainfall temperate environments (Fig. 3b). For eucalypts (Fig. 3a), allometry differed significantly ($P < 0.001$) between climates with regard to both slope and intercept, with the Tukey test indicated differences were attributable to allometry under low-rainfall climates being significantly different from those in high rainfall and tropical climates. However, inclusion of these climate categories within the model increased the amount of variation in above-ground biomass explained by <0.01 units. The relatively minor allometry differences between climatic regions contrasts with the findings of others (e.g. Brown et al., 1989; Sternberg and Shoshany, 2001; Drake et al., 2003; Chave et al., 2005; De Walt and Chave, 2004), many of which have attributed these differences to changes in tree wood density or structure (e.g. height to diameter ratios) with climate. The lack of agreement may be because these previous studies generally assessed a greater diversity of tree genera across a wider range of climatic conditions than were studied here.

3.2. Validation of allometry-predicted biomass

For each of the four types of equations developed, we compared estimated biomass versus measured biomass at the site-level through direct measurement from whole-plot harvesting (Fig. 5;

Table 7). Such comparisons have been made in northern hardwood forests in New Hampshire, USA (Arthur et al., 2001), and in mixed-species vegetation in the Sonoran Desert, Mexico (Búquez and Martínez-Yrízar, 2011). Our paper is the first report where bias of estimates from equations has been determined by testing against measured values across a wide range of sites and productivities.

Bias of generic equations was as high as 38–45% at some sites (data not shown, as only average bias across the eight direct measurement sites is given in Table 7). The absolute value of bias increased with increasing biomass. Such bias at sites where trees are large may be partly due to the high uncertainty of prediction for trees of high stem diameters (see 95% confidence intervals of prediction in Figs. 2–4). This could be attributed to: (i) high variability in biomass observed in large trees, together with the small-sample number, and (ii) linear equations developed on transformed data may not give due weighting to larger trees which contribute to a majority of site biomass. Further work is therefore required to increase the representativeness of larger trees in our equations, and to test the merits of using non-linear equations (e.g. Brown et al., 1989; Bi and Hamilton, 1998; Parresol, 1999; Ritsch and Sochacki, 2003; Bi et al., 2004; Búquez and Martínez-Yrízar, 2011; Morote et al., 2012).

The potential for high bias at a given site warrants attention when the objective is to obtain site-based prediction of biomass. However, when the objective is to obtain regional or estate average estimates of biomass, results from Fig. 5 and Table 7 show that across a range of sites, %*EBP* was less than 11% regardless of the allometry used. This was further confirmed by the fact that when tested on an individual tree or shrub basis (where above-ground biomass was at least 5 kg tree⁻¹) across a wider range of sites, biases of individual-based estimates of biomass were even less than that observed in the site-level analyses (Table 7).

Accuracy of predicted biomass, as quantified by *MSEP* and *EF*, were predominantly influenced by precision rather than bias. Further, when applying allometry to estimate biomass on a site-level compared to estimating regional biomass, precision is particularly important. As shown in Table 7, there was generally lower precision (i.e. higher standard deviation of residuals, *sd(e)*), and thus lower accuracy (i.e. higher *MSEP* and lower *EF*), with the application of equations which were not species-specific. When tested on either a site-basis or an individual-basis, inclusion of species-specific factors in generic equations increased *EF* by up to 0.08 units. Others studies also found that despite loss of precision with the application of generic equations, there were only minor (<0.06) decreases in *EF* and/or *R*² when generic rather than site-specific

equations were applied in woodlands (Williams et al., 2005), eucalypt plantations (Montagu et al., 2005), and secondary forests (van Breugel et al., 2011).

In summary, when predicting above-ground biomass at a site-level, application of species-specific equations (site-based or generic) is advisable given these provide the highest level of precision and accuracy. However, when estimating estate or regional level biomass, growth-habit, or universal, generic equations will be suitable as they provide un-biased estimates across a range of sites. Such generic equations may be particularly useful where: (i) only stem diameter data are available, (ii) harvesting is not permitted for conservation reasons, and commonly, (iii) resources are not available for biomass harvesting.

There are three important caveats to these recommendations to ensure they do not result in systematic biases. Firstly, despite the relatively high accuracy of generic species-specific equations, it is always good practice to verify any equations before applying them to a new region. Secondly, estimates of biomass from site-and-species specific equations may not necessarily be un-biased if the sample number is <20 trees (Paul et al., 2013b), or when site-specific equations are applied to a new sites with different attributes (Ximenes et al., 2006). Another caution relates to the domain of application of generic equations; they should be applied only within the regions from which data was derived to construct them (i.e. Clark and Clark, 2000). Constraining the domain of generalised equations is important because when the domain becomes large (e.g. pan-continental), verification fails (e.g. Madgwick et al., 1991; Basuki et al., 2009; Vieilledent et al., 2012). In our study, the domain was southern and eastern Australia (where >300 mm year⁻¹) for trees and shrubs with stem diameters within the range indicated (Tables 4 and 5). As the ages of plantings increase in Australia, generic equations need to be refined to account for the likely changes with age in wood density, and senescence and damage of large branches.

4. Conclusions

This study has advanced the development and testing of allometric equations of varying levels of generality for estimating above-ground biomass of mixed-species environmental plantings. Predicted above-ground biomass was tested against direct measurements from a range of sites. It was shown that when requiring regional- or estate-level estimates of biomass, application of generic equations developed here provide estimates which have percentage errors of biomass prediction of less than 11%. However at a given site, these errors could be as high as 45% when using generic equations. Further, precision, and thus accuracy, tended to decline (model efficiency decreasing by up to 8%) when generic equations were further generalised to be applicable to growth-habits as opposed to specific species. Generic equations which are species-specific appear to offer the best compromise between accuracy and cost-effectiveness.

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