

Testing the generality of below-ground biomass allometry across plant functional types



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ABSTRACT

Accurate quantification of below-ground biomass (BGB) of woody vegetation is critical to understanding ecosystem function and potential for climate change mitigation from sequestration of biomass carbon. We compiled 2054 measurements of planted and natural individual tree and shrub biomass from across different regions of Australia (arid shrublands to tropical rainforests) to develop allometric models for prediction of BGB. We found that the relationship between BGB and stem diameter was generic, with a simple power-law model having a BGB prediction efficiency of 72–93% for four broad plant functional types: (i) shrubs and *Acacia* trees, (ii) multi-stemmed mallee eucalypts, (iii) other trees of relatively high wood density, and; (iv) a species of relatively low wood density, *Pinus radiata* D. Don. There was little improvement in accuracy of model prediction by including variables (e.g. climatic characteristics, stand age or management) in addition to stem diameter alone. We further assessed the generality of the plant functional type models across 11 contrasting stands where data from whole-plot excavation of BGB were available. The efficiency of model prediction of stand-based BGB was 93%, with a mean absolute prediction error of only 6.5%, and with no improvements in validation results when species-specific models were applied. Given the high prediction performance of the generalised models, we suggest that additional costs associated with the development of new species-specific models for estimating BGB are only warranted when gains in accuracy of stand-based predictions are justifiable, such as for a high-biomass stand comprising only one or two dominant species. However, generic models based on plant functional type should not be applied where stands are dominated by species that are unusual in their morphology and unlikely to conform to the generalised plant functional group models.

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1. Introduction

Both above-ground biomass (AGB) and below-ground biomass (BGB) contribute to the woody vegetation sink within the global carbon budget (Le Quéré et al., 2015). Climate change may result in shifts in the ratio of tree BGB to AGB (e.g. via changes in water deficit that affect partitioning or the size distribution of trees), with far-reaching consequences for the global carbon budget (Ledo et al., 2018). However, BGB cannot be quantified using remote sensing metrics as has been done for the AGB component (Haverd et al., 2013; Mitchard et al., 2013; Chen et al., 2015). Therefore, the development of models to explain BGB is critical to informing predictions of biomass yields or biomass carbon stocks (Richards and Evans 2004).

BGB can be estimated from AGB at either an individual- or stand-level through the use of root-to-shoot ratios (BGB:AGB, Ledo et al., 2018), and this approach has merit when broad-scale AGB estimates are obtained via remote sensing products rather than via field-based assessments. However, this approach has limitations. Estimating BGB based on predictions of AGB are subject to relatively high uncertainties; for example, mean absolute prediction error of AGB was 15–39% and 13% at the individual- and stand-level, respectively, for plant functional types across the Australian continent (Paul et al., 2016). In contrast, if BGB of an individual is predicted by applying verified allometric models to field measurement of stem diameter (D) measured at a specified height above the ground, the uncertainty is likely to be much lower because errors in D estimation are relatively small (e.g. 2–7%, Paul et al., 2017). Moreover, BGB:AGB defaults obtained from the average of multiple stands of a given ecosystem (Mokany et al., 2006) do not explicitly account for variations in stand density and the mix of species; both of which influence BGB (Westman and Rogers, 1977; Bernardo et al., 1998; Ritson and Sochacki, 2003; Xue et al., 2011; Gonzalez-Benecke et al., 2014). Stand-based estimates of BGB, resulting from application of allometric models with D as a predictor variable to each individual within a stand, may inherently account for stand density and species-mix.

When developing allometric models for prediction of BGB of woody plants, it is unclear to what extent data should be pooled or separated according to their morphological, phylogenetic and/or phenological characteristics; variation often encapsulated by classification of species into plant functional types. It is also unclear whether the inclusion of stand characteristics or bioclimatic variables improves the performance of BGB allometric models compared with using D alone. A true test of

the accuracy of such models is direct validation at the stand-level by comparing allometry-predicted BGB against that measured through whole-plot excavation. Although such stand-level validation has been undertaken previously by Paul et al. (2014) for young plantings in southern Australia, no such validation has been undertaken for more broadly-applicable BGB allometric models derived from root data sampled from both planted and natural systems, and across a range of stand ages and ecosystem types.

Australia provides a good case study for testing generalised allometric models given its long history of research contributions to BGB data sets (e.g. Forrest, 1969; Baldwin and Stewart, 1987; Applegate, 1982) spanning a broad range of ecoregions (i.e. arid shrublands to tropical rainforests) with plant functional types ranging from shrubs and short multi-stemmed trees to some of the largest trees in the world (Sillett et al., 2015; Specht and Specht, 2002, 2013). Improving the assessment of Australia's vegetation carbon sink is of global importance as the high inter-annual variability that is characteristic of the global vegetation sink is in large part due to variability in the carbon capture of the semi-arid ecosystems of Australia (Houghton et al., 2012; Poulter et al., 2014; Ballantyne et al., 2015).

Here we collated destructively-measured BGB datasets from individual trees and shrubs sampled from a broad range of stands from differing climatic regions of Australia, including those in natural ecosystems or otherwise established through human intervention (i.e. planted). We then analysed this data set to assess whether D -based allometric models of BGB were improved: (i) when based on species rather than plant functional groups; and (ii) by the inclusion of stand characteristics (age and management) or climatic variables. Our objectives were to recommend the most appropriate allometric model(s) for estimating BGB in ecosystems across the Australian continent, and to quantify the accuracy of the recommended model(s) when tested against direct measurements of stand-level BGB obtained using whole-plot excavation across a range of contrasting sites. The recommended models for predicting BGB were applied together with those previously recommended for prediction of AGB (Paul et al., 2016) to provide estimates of BGB:AGB ratios for plant functional types of differing allometry.

2. Methods

2.1. Data set

2.1.1. Data compilation

Data sets of BGB from destructive harvesting of 2054 individual

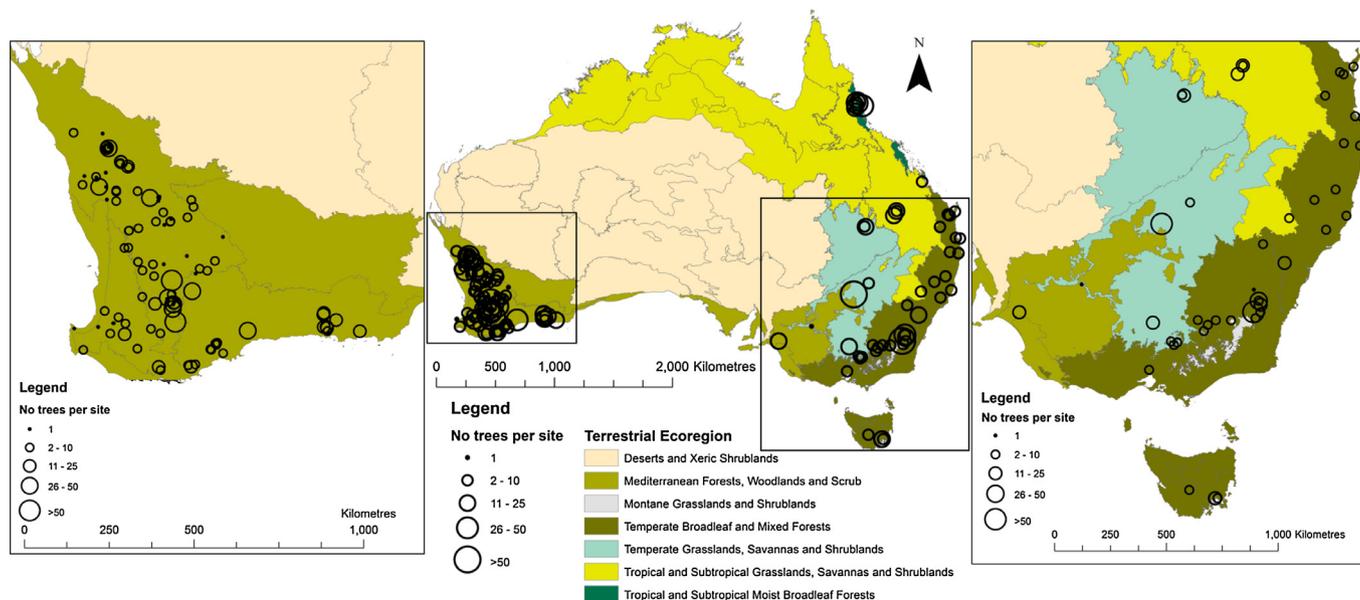


Fig. 1. Location of trees or shrubs sampled for biomass by terrestrial ecoregion across Australia (DSWPC, 2015).

trees and shrubs were obtained from 38 published and unpublished sources (Paul et al., 2018a). These were from a range of managed and natural woody ecosystems across 210 sites in various Australian ecoregions (Fig. 1).

BGB was defined as tree and shrub roots of > 2 mm in diameter extracted from a soil depth of 2–3 m, including stem biomass to a height of 10 cm above ground (i.e. the ‘stump’). This method of root extraction ensured the majority of root biomass was captured because: (i) fine roots (< 2 mm) of woody plants only comprise 8–14% of the total root biomass, depending on the AGB (Applegate, 1982; Misra et al., 1998; Li et al., 2003; Mokany et al., 2006), and (ii) typically 95% of all roots are found within 2 m of the ground surface (Schenk and Jackson, 2002). The stump was included in the calculation of BGB because 10 cm is a common height targeted in operational harvesting, and hence, remains together with the roots as part of the unharvested biomass.

When sampling for BGB, sub-samples (0.5–25 kg each, depending on the size of the individual) were used for percentage moisture content determination, with the lignotuber and/or root stump sampled separately from other coarse roots. These sub-samples were oven-dried at 70 °C to constant weight, with the estimates of moisture content of components used to calculate the total dry weight of BGB (kg dry matter (DM) of an individual plant).

Each tree or shrub excavated also had a measure of stem diameter (D , measured over bark). For single-stemmed trees, D was measured at 130 cm height above ground level (D_{130}); the most common international standard (e.g. Picard et al., 2012). However, for shrubs and small multi-stemmed trees where D_{130} measurements introduced errors due to the presence of multiple stems at this height, or where the individual was too small to have a measurable D_{130} , the D of each stem was typically measured at 10 cm height above the ground (D_{10}). For multi-stemmed individuals, a single, pooled D estimate was obtained from the diameter equivalent representing the sum of the cross-sectional areas of each of the individual stems.

2.1.2. Functional groups

The data set included 128 species. Only seven species (*Eucalyptus polybractea*, *E. loxophleba*, *E. kochii*, *E. globulus*, *E. occidentalis*, *Pinus pinaster* and *P. radiata* D. Don) were sampled in sufficient numbers ($N > 100$ individuals) to have confidence in developing species-specific models that are likely to reflect the true population (i.e. targeted coefficient of variation in predicted BGB being ca 5%; Roxburgh et al.,

2015). This relatively high sample size requirement was based on the assumption that, due to measurement errors being relatively high when extracting roots from the soil, BGB allometric models are likely to have a relatively high inter-sample variability, with residual standard deviations of about 0.50.

Because the sample size of most (95%) species was insufficient to assess the allometry of BGB at a species-specific level, we categorised all species in the data set into plant functional types of unique physiognomic growth form (Gitay and Noble, 1997), i.e. groupings of plant species with distinctive branch architecture and/or stem wood density. There is evidence that such an approach negates the need to explicitly account for stem wood density in allometric models of biomass for Australia (Paul et al., 2016). Consistent with species groupings used in allometric models of AGB by Paul et al. (2016), the groups used for BGB were:

- i. $F_{Shrub\&Ac}$. Shrubs and small multi-stemmed trees. This group included the common Australian genus *Acacia* (36% of the $F_{Shrub\&Ac}$ data set), which comprised both shrub (31%, e.g. *A. hemiteles*, *A. murrayana* and *A. victoriae*) and small tree (69%, e.g. *A. saligna*, *A. acuminata* and *A. aneura*) forms. The group also included another 18 genera of shrubs (generally < 2 m height), with the most common genera being *Eremophila*, *Dodonaea* and *Melaleuca*.
- ii. F_{Mallee} . Multi-stemmed (mallee) trees from the genus *Eucalyptus*, which commonly have a lignotuber and relatively high wood density: mean \pm standard deviation (SD) $0.88 \pm 0.08 \text{ g cm}^{-3}$, largely (93%) based on estimates from the global stem density database (Chave et al., 2009; Zanne et al., 2009), with the remainder being directly measured. This group included 17 species, with the most common being those typically established in monoculture plantings, such as *E. loxophleba* subsp. *lissophloia* (41%), *E. polybractea* (24%) and *E. kochii* subsp. *plenissima* and subsp. *borealis* (18%). Other common species included *E. loxophleba* that were not subsp. *lissophloia*, *E. porosa*, and *E. platypus*.
- iii. F_{Tree} . Typically single-stemmed trees of relatively high wood density: mean \pm SD $0.69 \pm 0.16 \text{ g cm}^{-3}$, largely (80%) based on estimates from the global stem density database, with the remainder being directly measured. This group included 35 genera, most commonly *Eucalyptus* (or the closely-related *Corymbia*) (77%) from either hardwood plantations or native forests or woodlands. Other well-sampled species included the introduced *Pinus pinaster* (14%),

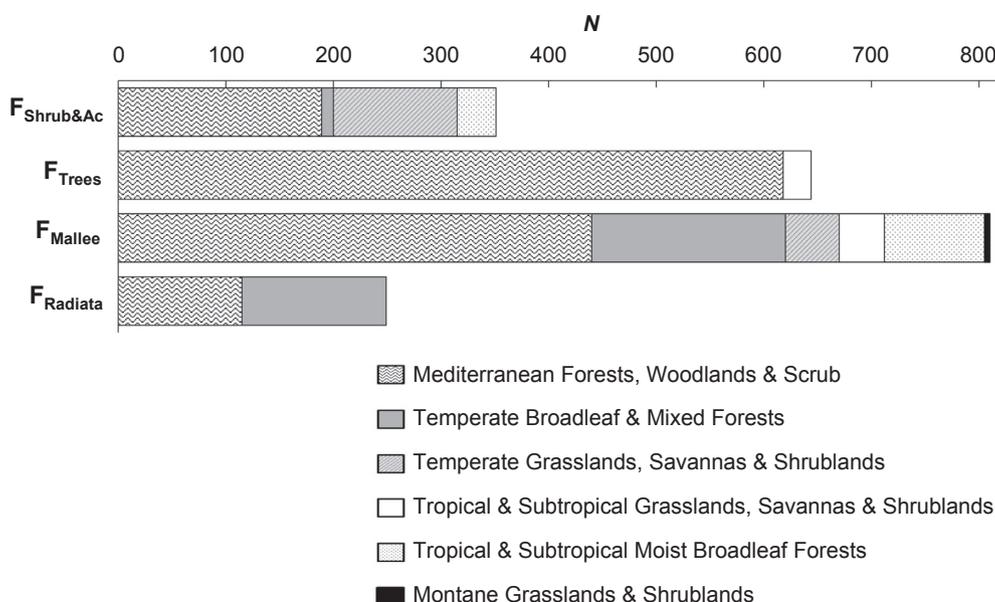


Fig. 2. Number of individuals (N) sampled of each of the four plant functional types by ecoregion (defined in Fig. 1).

which is a common low-rainfall plantation species in Australia. There was a large diversity of genera sampled from the tropical ecoregion, with the most common being species from the genus *Argyrodendron*.

- iv. *F_{Radiata}*. The specific tree species *Pinus radiata*, of relatively low stem woody density: mean \pm SD $0.40 \pm 0.04 \text{ g cm}^{-3}$, largely (86%) based on estimates from the global stem density database, with the remainder being directly measured. This species is the most common species in softwood plantations within high rainfall regions of temperate Australia.

The *F_{Shrub&Ac}*, *F_{Mallee}*, *F_{Tree}*, and *F_{Radiata}* groupings comprise about 20, 30, 40 and 10% of the data set respectively. The geographical extent of the Australian terrestrial ecoregions is shown in Fig. 1, and the representation of these ecoregions in the sampling for each plant functional type is shown in Fig. 2. The ‘Mediterranean forests, woodlands and scrub’ was the most well represented ecoregion (66%).

2.1.3. Harmonisation of BGB data estimates

Because measurement of BGB is resource-intensive and challenging, among the 38 studies used to build the data set (Paul et al., 2018a), various protocols were utilised, based on the resources available and the type of ecosystem sampled. The most common protocol (51% of data) included the stump in the BGB sampling and excavated the area around the individual to the mid-point boundaries with neighbouring trees, termed ‘Voronoi polygons’ (Wildy and Pate, 2002; Saint-André et al., 2005). Three other protocols were used for the remaining 49% of the data set. For 20% of the data set where the stump was included with the AGB, stump biomass was estimated using empirical data as described by Paul et al. (2014), and added to the BGB. For 15% of the data set, where BGB was excavated in a set area (generally 4 m^2 around a tree base), based on empirical evidence (Paul et al., 2014), we assumed that only 70.2% of BGB was excavated and so an additional 29.8% was added to the BGB sampled. Finally, for 14% of the data set, where excavation of the BGB of individuals was not possible due to the close spatial association of the target individual with nearby individuals (known as ‘clustering’), relatively large areas ($50\text{--}200 \text{ m}^2$) were excavated and the BGB of the entire vegetation ‘cluster’ was provided. Although root stumps belonging to each individual could be identified, the remaining coarse roots were allocated to each individual within the ‘cluster’ in accordance with its proportional contribution to the total AGB measured for that ‘cluster’.

As quantified by Paul et al. (2014), uncertainties in allometry-predicted BGB result from assumptions required to harmonise the BGB data sets derived from alternative protocols. These uncertainties may be reduced as additional data becomes available to inform the adjustment factors applied, e.g. varying the adjustment factor for set area excavation based on the size of the tree and/or the stand density.

Table 1

Characteristics collated for the entire data set (*All_{Universal}*), or for each of the four categories of plant functional types. (*F_{Shrub&Ac}*, *F_{Mallee}*, *F_{Tree}*, and *F_{Radiata}*). Abbreviations as follows: ‘*N* individuals’, total number of individuals; ‘*D₁₀*’ and ‘*D₁₃₀*’, mean stem diameter measured over bark at 10 cm and 130 cm height above the ground respectively; ‘*N* stands’, number of stands from which the trees or shrubs were harvested; ‘*N* spp.’, number of species that were sampled; ‘%Age < 20 yrs’, percentage of individuals from stands with age < 20 years; ‘%Managed’, percentage of individuals from stands that were managed rather than naturally regenerated without human intervention; ‘MAT’, long-term mean annual temperature, averaged across sites from which individuals were sampled; and ‘MAR’, long-term mean annual rainfall, averaged across sites from which individuals were sampled. Where relevant, standard deviations (and for *D₁₀* and *D₁₃₀*, the range in values) are provided in parentheses.

Type	<i>N</i> individuals	<i>D₁₀</i> (cm)	<i>D₁₃₀</i> (cm)	<i>N</i> stands	<i>N</i> spp.	%Age < 20 years	%Managed	MAT (°C)	MAR (mm yr ⁻¹)
<i>All_{Universal}</i>	2 054	17.0 (19.6; 0.6–177.0)	NA	210	128	72.0	77.4	16.9 (2.5)	591 (510)
<i>F_{Shrub&Ac}</i>	351	11.8 (10.6; 0.6–98.4)	NA	45	33	41.0	43.0	18.8 (2.0)	532 (496)
<i>F_{Mallee}</i>	644	11.8 (10.0; 1.0–81.1)	NA	100	17	88.8	97.2	17.0 (1.5)	393 (75)
<i>F_{Tree}</i>	810	24.4 (27.1; 2.1–177.0)	18.9 (21.2; 1.1–138.8)	72	77	65.8	69.5	16.7 (2.9)	781 (683)
<i>F_{Radiata}</i>	249	13.8 (8.8; 3.6–49.6)	9.8 (7.8; 1.4–41.4)	4	1	92.4	100.0	14.6 (1.8)	569 (211)

2.1.4. Ancillary stand and site data

Data about the stand and site from which an individual was sampled were collated (Table 1). Stand variables included whether the site was ‘natural’ (i.e. naturally-regenerated shrubland, woodland or forest) or managed (i.e. human-induced establishment from planting of nursery stock, direct seeding or human-induced natural regeneration), and whether the stand was younger than 20 years. There was insufficient replication, and/or confidence in exact ages, to facilitate further age-class groupings. Site factors included long-term mean annual rainfall (MAR, mm yr⁻¹) and mean annual temperature (MAT, °C) (BoM, 2015; 1970–2015, 2.5 km resolution).

2.1.5. Standardising diameter estimates, and outlier checking

For many individuals in the data set, *D* was measured at multiple heights, thereby allowing derivation of generic relationships for prediction of *D* at a given height based on *D* measured at another height (see empirical linear relationship between *D* measured at different heights given in Table S2 of Paul et al., 2016). These relationships were used to ‘gap-fill’ *D* estimates as required, with *D₁₃₀* or *D₁₀* being estimated for 28% of the 2 054 individuals within the data set.

Very small individuals (*D₁₀* < 0.6 cm and *D₁₃₀* < 1.1 cm) were not included in the database because they were considered unlikely to conform to biomass scaling laws typical of woody plants due to relatively little secondary thickening (Niklas, 2004; Enquist et al., 2007). Data for a further 38 individuals from 10 sites (and six sources) were excluded as outliers as their measured BGB fell outside the 99.9% confidence interval of prediction of the mean of the appropriate plant functional type model. These outliers were removed on the basis that they were highly unlikely to have the reported values of BGB for the measured dimensions.

2.2. Allometric model

The simple power-law allometric model was used to predict BGB of an individual tree or shrub based on the explanatory variable, *X* (Eq. (1)). Eq. (1) was linearized by natural logarithmic transformation (Eq. (2)) so that coefficients (*a* and *b*) could be estimated using ordinary least squares linear regression analyses, with data corrected for heteroscedasticity, such that residual errors were normally distributed on the logarithmic scale (ϵ ; which becomes a multiplicative error in the power model, ϵ' , Picard et al. (2012)):

$$\text{BGB} = a \times X^b \times \epsilon' \quad (1)$$

$$\ln \text{BGB} = \ln a + b \times \ln X + \epsilon \quad (2)$$

Eq. (2) was applied to model the entire dataset (universal model, *All_{Universal}*), and to the data sets of the four plant functional types: *F_{Shrub&Ac}*, *F_{Mallee}*, *F_{Tree}* and *F_{Radiata}*. The simplest form of Eq. (2) had *X* = *D*, where *D* is *D₁₀* or *D₁₃₀* for *F_{Tree}* and *F_{Radiata}*, and by necessity, *D₁₀* for *F_{Shrub&Ac}* and *F_{Mallee}*, and hence, *All_{Universal}*.

When back-transforming from the logarithmic to the natural scale, a

correction factor (CF) is required to remove bias in biomass estimates. A review of nine CFs (Clifford et al., 2013) recommended the MM CF (Minimize Mean Square Error CF, Shen and Zhu, 2008) for predicting biomass of new trees or shrubs as it gave relatively low prediction bias. Because the value of the MM CF varies with D , a range of MM CF values are reported. The more commonly used Baskerville CF (Baskerville, 1972), which assumes the variability is constant across D , may lead to biased estimates of biomass, particularly for individuals with a D that is appreciably larger or smaller than the mean D used to develop the allometric model. In this study the MM and Baskerville CFs were consistent, at least to one decimal place, due to our large sample sizes; and therefore we report both the MM and Baskerville CF.

2.3. Statistical analysis

2.3.1. Model checking and selection criteria

To confirm the validity of tested models, we checked that there was no heteroscedasticity through examination of probability and quantile plots of the residuals. Then, the performance of valid models of lnBGB (Eq. (2)) was quantified using five fit statistics: (i) standard errors of the coefficients $\ln a$ and b , (ii) residual mean square error, $RMSE$, (iii) adjusted coefficient of determination, R^2 , (iv) Akaike's information criterion (AIC , Burnham and Anderson, 2004), where the lowest AIC indicated the most parsimonious model, and to further aid comparisons among alternative models of differing numbers of parameters, (v) the Mallows' C_p statistics (Mallows, 1973), where a C_p higher than the number of explanatory variables indicated poor model fit.

Using back-transformed BGB predictions, the predictive performance was quantified by: (i) model efficiency, expressed as a proportion (EF , Soares et al., 1995), where 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, and (ii) average bias, or mean of the residuals expressed in absolute terms and provided as a proportion (%) of the observed value (i.e. mean absolute prediction error, 'MAPE', using back-transformed BGB predictions) (Sileshi, 2014).

2.3.2. Alignment of plant functional groupings for BGB and AGB allometries

To facilitate the application of allometric models of both AGB and BGB to various stands across Australia, the sub-categories of plant functional groupings used for BGB were consistent with those applied for allometric models of AGB (Paul et al., 2016, see Fig. S1). General linear modelling (GLM) was used to assess whether lnBGB prediction from ln D was significantly influenced by species group, and if so, which species groupings had statistically ($P < 0.05$) unique BGB allometry. Although alternative statistical approaches are available for testing whether species or groups of species have statistically-significant allometry, these provided results consistent with GLM (Paul et al., 2018b). Plant species typically measured at D_{10} (shrubs and multi-stemmed trees) required separate allometric models to those typically measured at D_{130} (single-stemmed trees), hence, analysis of unique functional sub-categories was undertaken for both of these broad groups of species. From the eight species groups, four categories of plant functional types were required for BGB allometric models ($F_{Shrub\&Ac}$, F_{Mallee} , F_{Tree} and $F_{Radiata}$) (Fig. 3).

2.3.3. Effect of level of generalisation on BGB prediction accuracy

Data from the seven tree species with $N > 100$ (*E. polybractea*, *E. loxophleba*, and *E. kochii*, *E. globulus*, *E. occidentalis*, *P. pinaster* and *P. radiata*) were used to assess whether the fit in BGB predictions (i.e. prediction accuracy) improved as the specificity of the allometric models increased (i.e. $All_{universal}$ model cf. functional-type model cf. species-specific model). Large samples sizes were required to target a 5% coefficient of variation prediction of biomass when applying allometric models of relatively high variability, as anticipated for BGB (i.e. residual standard deviations 0.47–0.50; Roxburgh et al., 2015). Further, data for the shrub species *Dodonaea viscosa* subsp. *angustissima* and *Eremophila sturtii* ($N = 49$ – 51 , indicating a coefficient of variation of prediction of about 7%, Roxburgh et al., 2015), were used to explore whether the application of the generalised multi-species $F_{Shrub\&Ac}$ model generated significant bias in BGB when compared to a species-specific model.

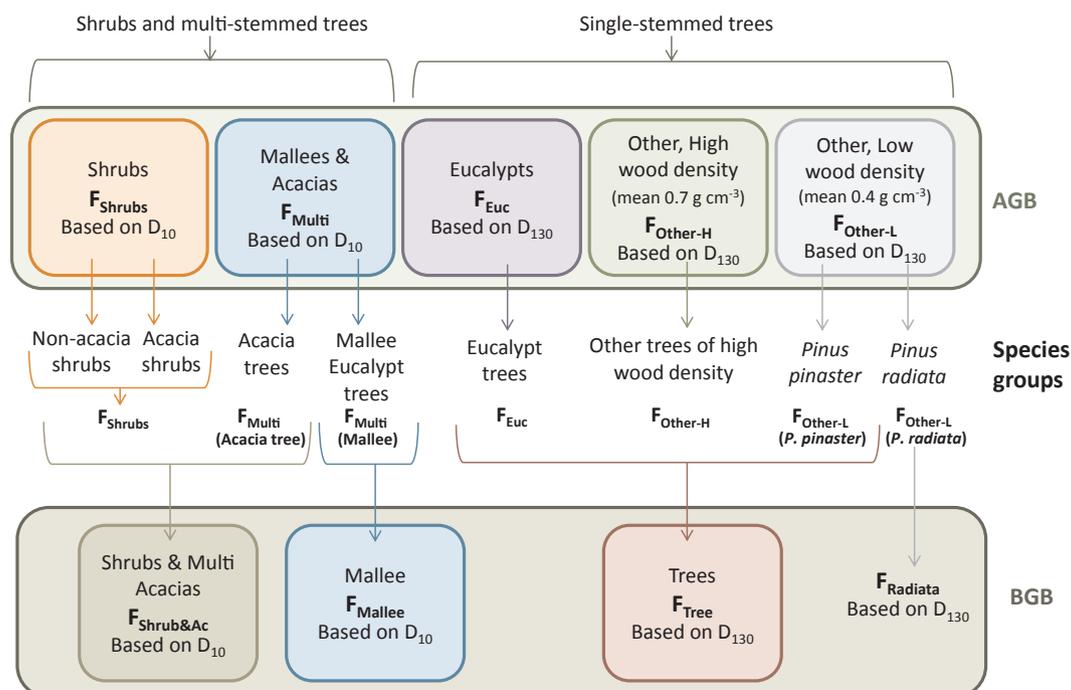


Fig. 3. Groupings of plant species into plant functional types as applied in AGB generic allometric models (Paul et al., 2016), and how these relate to the grouping of plant species into the plant functional types used here for BGB generic allometric models.

2.3.4. Effect of stand and site factors on BGB allometry

GLM was used to assess whether inclusion of stand or site factors improved the performance of Eq. (2), as indicated by an improvement in the fit statistics. The stand and site factors tested included: (i) stand age (< 20 years or ≥ 20 years), (ii) management (natural or managed vegetation), (iii) ecoregion (as per Fig. 2), (iv) MAT, and (v) MAR. Interactions of these site-factors with lnD were included in the model only where these were significant ($p < 0.05$).

Within our data set (Table 1), data for the single-stemmed tree species *Eucalyptus populnea* was the most suitable for comparison between ecoregions, because the sample sizes of 20–36 indicated coefficients of variation of allometry-predicted biomass of only 8–11% (Roxburgh et al., 2015). These data provided a case study testing the effect of ecoregion on the F_{Tree} model across: (i) ‘Temperate Grasslands, Savannas and Shrublands’, where MAR was 400–460 mm ($N = 20$, collated from two stands), and (ii) ‘Tropical and Subtropical Grasslands, Savannas and Shrublands’ where MAR was 600–1 070 mm ($N = 36$, collated from three stands).

2.4. Model validation using whole plot root excavation

Data from 11 stands of varying structure and from contrasting environments (Table 2) where whole plots were excavated to obtain ‘true’ and direct measurements of stand-scale BGB (Paul et al., 2014), were used to test the accuracy of allometric models. We applied the generic $F_{Shrub&Ac}$, F_{Mallee} and F_{Tree} models of best fit (Eq. (2), using D as the predictor variable) to inventories of D obtained from each of these 11 stands. The allometry-predicted BGB of all individuals within the plots was then summed to provide a predicted BGB at the stand-level. We calculated the resulting prediction quality statistics of EF , $MAPE$ and $RMSE$. To determine whether there was any improvement in model performance when less generalised models are applied, this analysis was repeated with the use of species-specific models when they were available (Table S1).

2.5. BGB:AGB

The allometric models developed for BGB, and those developed by Paul et al. (2016) for AGB, were applied to predict the BGB:AGB ratio for the different sub-categories of plant functional types (Fig. 3). For the 1 990 individuals in the data set where both AGB and BGB were measured, we compared predicted BGB:AGB ratio with that observed, and the mean (\pm SD) allometry-predicted BGB:AGB between the different

species groups. We also explored the relationship between allometry-predicted BGB:AGB and the D of an individual tree or shrub.

3. Results

3.1. Allometric models

The model (Eq. (2)) predicted BGB with good accuracy for four categories of plant functional types: $F_{Shrub&Ac}$, F_{Mallee} , F_{Tree} , and $F_{Radiata}$ (Fig. 4a, d, g, j). The models explained 90–97% of the variation in lnBGB, with errors ($RMSE$) of 0.26–0.55 (Table 4). When lnBGB was back-transformed and bias corrected, there was relatively high uncertainty in the prediction of BGB for a given tree or shrub for a given D (see 95% confidence intervals of prediction, Fig. 4b, e, h, k). However, these individual errors tend to cancel out when predictions are made across a large number of individuals. The generalised models provided reasonable accuracy across the data sets, giving an efficiency of prediction of BGB of 72–93%, with a $MAPE$ range of 21–55% (Fig. 4c, f, i, l; Table 3).

For F_{Tree} and $F_{Radiata}$ models, there was no consistent difference in fit statistics when the model (Eq. (2)) used the explanatory variable D_{10} instead of D_{130} (Table 3). However, for $F_{Radiata}$ models using ln D_{130} , it was necessary to exclude trees with $D_{130} < 5.0$ cm to avoid positive bias in predictions of larger ($D_{130} > 30$ cm) trees.

The performance of the $All_{Universal}$ model was relatively poor (efficiency of prediction of BGB only 74%, Fig. S1a) because it generalises across plant functional types with substantially different BGB allometry (Fig. S1b and c). GLM demonstrated that allometry of mallee eucalypts was significantly different ($p < 0.001$) to that of shrubs and other multi-stemmed trees (e.g. *Acacia* species) (Fig. S1c and d), while allometry of *Pinus radiata* was significantly different ($p < 0.001$) to that of other single-stemmed trees (Fig. S1d, e). These results justify splitting the universal model into four plant functional type models (Table 3, Fig. 4).

The application of alternative models to the seven species that were adequately sampled ($N > 100$, Table S1) showed that the predictive performance generally increased with increasing model specificity: universal *cf.* plant functional type *cf.* species-specific. When compared to the application of the universal model, the application of more specific models generally increased the efficiency of prediction of BGB by up to 15–17%, and decreased the $MAPE$ by up to 16–50% (Table 4). There were some exceptions, with the application of the $All_{Universal}$ model to *P. radiata*, or the application of F_{Mallee} to *E. kochii*, resulting in

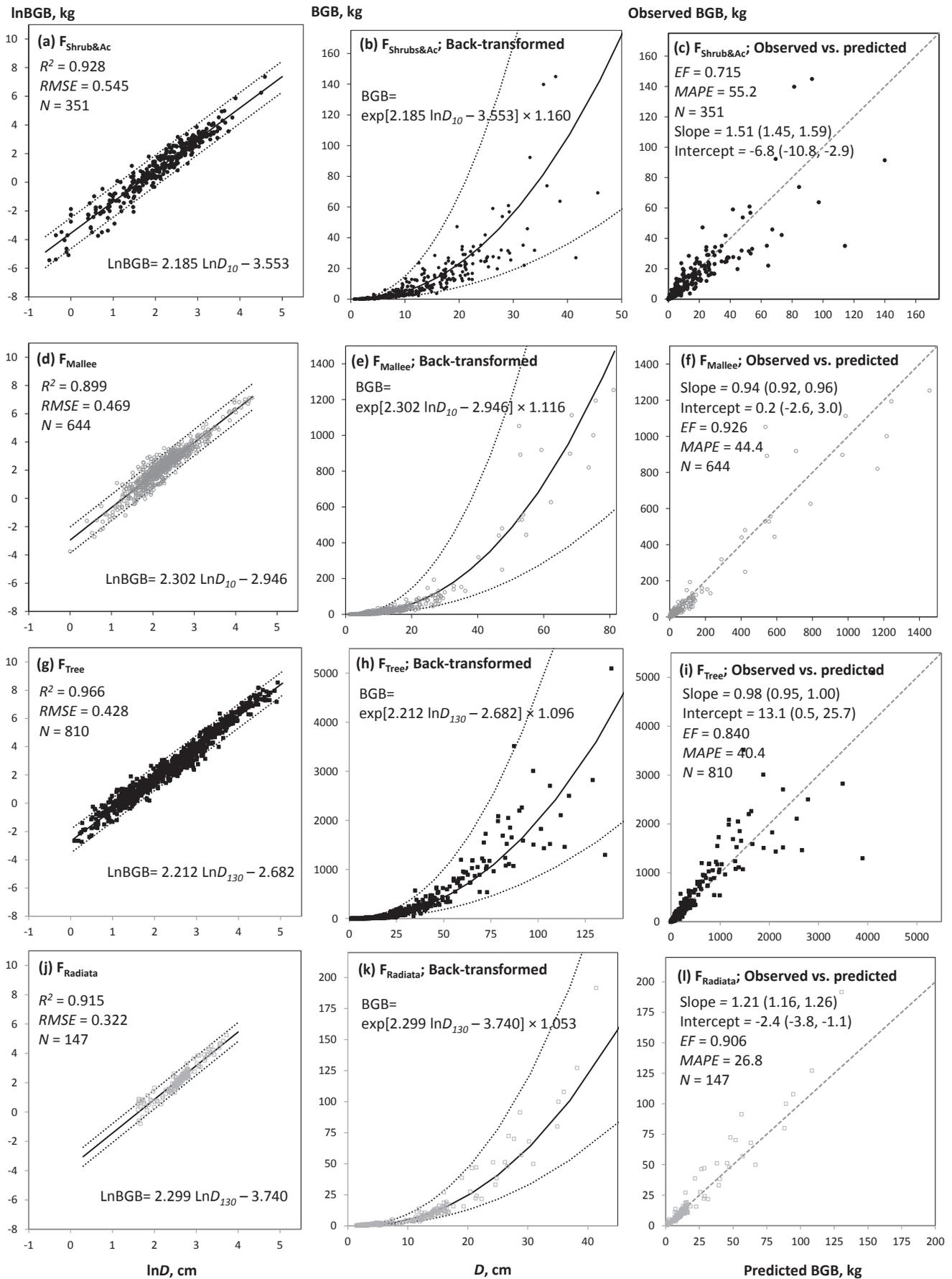
Table 2

Summary of the main characteristics of 11 contrasting stands where whole-plot BGB excavation was used to test the accuracy of generalised allometric models based on plant functional type. Modified from Paul et al. (2014). Abbreviations as follows: ‘MAR’, long-term (1970–2015) mean annual rainfall; ‘Tree N ’, number of live trees or shrubs measured; ‘Type of stand’, where A refers to ‘Belt monoculture planting of the mallee eucalypt species *E. loxophleba* subsp. *lissophloia*’, B refers to ‘Block monoculture planting of the mallee eucalypt species *E. loxophleba* subsp. *lissophloia*’, C refers to ‘Belt planting of mixed-species’, and D refers to ‘Block planting of mixed-species’.

Site	Location (decimal degrees)	MAR (mm yr ⁻¹)	Age (year)	Tree N	Stand-scale AGB (Mg DM ha ⁻¹)	Stand-scale BGB (Mg DM ha ⁻¹)	Type of stand
Strathearn	–35.0485 S, 149.2325 E	637	15	371	38.9	25.30	C
Moir	–34.2809 S, 118.1820 E	439	20	346	42.4	17.07	C
Jenharwill	–36.3958 S, 144.4304 E	406	12	163	69.1	21.34	D
Gumbinnen	–36.2447 S, 141.8148 E	347	10	305	19.1	4.48	C
McFall	–33.7290 S, 117.3217 E	438	15–24	313	189.6	76.00	D
Leos	–37.8381 S, 147.7582 E	626	16	96	113.6	44.94	D
Pepal [#]	–33.4865 S, 117.7912 E	406	11	77	20.87	14.77	B
Bird [#]	–32.8515 S, 117.5892 E	376	11	41	37.68	18.27	B
Quicke [#]	–32.6736 S, 118.2361 E	339	14	29	77.63	37.79	B
Temby [#]	–33.1457 S, 117.7187 E	353	16	44	22.61	12.32	A
Angel [#]	–30.1970 S, 117.1160 E	297	16	34	9.93	9.78	A

[#] Species-specific allometric model for *Eucalyptus loxophleba* (Table S1) was applied as an alternative to the F_{Mallee} model.

[^] Species-specific allometric model for *E. occidentalis* (Table S1) was applied as an alternative to the F_{Tree} model for this species, although within this mixed-species stand, *E. occidentalis* only comprised 6% of the individuals sampled, or 16 individuals out of the 275 individual trees or shrubs excavated for direct measurement of stand-level BGB.



(caption on next page)

Fig. 4. Generic allometric equations for prediction of BGB from stem diameter (D , cm) of (a–c) shrubs and acacia trees ($F_{Shrub&Ac}$, where D was at 10 cm, D_{10}), (d–f) multi-stemmed mallee eucalypt trees (F_{Mallee} , where D was at 10 cm, D_{10}), (g–i) single-stemmed trees (F_{Tree} , where D was at 130 cm, D_{130}), and (j–l) *Pinus radiata* tree species ($F_{Radiata}$, where D was at 130 cm, D_{130}). There were three plots for each plant functional type: (a, d, g, j) indicating Eq. (2) fitted to the lnBGB data set, (b, e, h, k) indicating accuracy of the back-transformed and biased corrected model, and (c, f, i, l) indicating observed vs. predicted BGB. Black solid lines represent the model of best fit, dotted lines the 95% prediction interval, and dashed lines the 1:1 line. Values in parentheses are the 95% prediction interval of the slope and intercept. NB: To improve the clarity of the figure, panels (b) and (c) excluded three observations of the relatively large (D_{10} of 49–98 cm, and height of 17–20 m) *Acacia* trees sampled from the wet tropics.

substantial bias (*MAPE* 100–226%) (Table 4). Investigation of BGB allometry for two shrub species (Fig. 5), showed that one species had a slight bias in prediction of BGB when the generic $F_{Shrub&Ac}$ model was applied (mean bias + 2.3 kg for *D. viscosa* subsp. *angustissima*), but with bias being negligible for the other species (< 0.5 kg, *E. sturtii*) (Fig. 5a and b). Indeed, compared with application of the $F_{Shrub&Ac}$ model to predict BGB of *D. viscosa* subsp. *angustissima*, where prediction efficiency was only 13% and *MAPE* was 73%, the performance was much better for *E. sturtii*, where efficiency of prediction was 90% and *MAPE* only 33%.

3.2. Inclusion of stand and site-factor predictor variables

When compared to using D alone, including stand-factors (age and management) resulted in only minor model improvements, with the increase in explained variation of lnBGB being consistently < 2% (Table 5). Furthermore, for plant functional types where a majority of the individuals were from planted stands (e.g. F_{Mallee} and $F_{Radiata}$), there were insufficient data from natural stands to statistically ascertain any impact of management on BGB allometry. Accounting for ecoregion, MAT or MAR also resulted in relatively small model improvements, with the increase in explained variation being < 3% (Table 5). These findings were reinforced by observed negligible difference in BGB allometry for the one species (*E. populnea*) that was reasonably well sampled from two contrasting climates and ecoregions (Fig. 5c, d).

3.3. Model validation using whole-plot root excavation

Comparison of allometry-predicted BGB to observed BGB from direct whole-plot excavation across 11 contrasting stands (Table 2), showed prediction of stand-level BGB was good overall (efficiency of prediction 93%, *MAPE* 20.4%, Fig. 6). When this validation was repeated with application of species-specific models (where available), there was negligible difference in the accuracy of stand-level BGB prediction, with efficiency of prediction and *MAPE* both changing by less than one percent (Fig. S2 cf. Fig. 6).

Table 3

The fitted coefficient (and their standard errors) and fit statistics of generalised allometric models for BGB of the form given in Eq. (2), and using a predictor of D measured at 10 cm height (D_{10}) or 130 cm height (D_{130}). Here *RMSE*, R^2 , *CF*, *EF*, *MAPE*, and N refer to the standard error of the linear regression, adjusted coefficient of determination, bias correction factor, model efficiency (based on back-transformed BGB predictions), mean absolute percentage error (based on back-transformed BGB predictions), and sample size, respectively. All models fitted were highly significant ($P < 0.001$). The diameter range relevant to each model is indicated in brackets (assuming a minimum D_{10} of 0.6 cm, and a minimum D_{130} of 1.1 cm). Parameters and performance of the species-specific allometric models are provided in the Table S1.

Model	ln(a)	b	MM CF [*]	Baskerville CF [†]	RMSE	R ²	EF	MAPE	N
$All_{Universal}$ ($D_{10} < 177$ cm)	-3.524 (0.045)	2.295 (0.017)	1.2373–1.2421	1.2426	0.659	0.896	0.735	78.9	2 054
$F_{Shrub&Ac}$ ($D_{10} < 98$ cm)	-3.553 (0.075)	2.185 (0.033)	1.0782–1.1508	1.1601	0.545	0.928	0.715	55.2	351
F_{Mallee} ($D_{10} < 81$ cm)	-2.946 (0.071)	2.302 (0.031)	1.1047–1.1154	1.1160	0.469	0.899	0.926	44.4	644
F_{Tree} ($D_{10} < 177$ cm)	-3.854 (0.046)	2.389 (0.016)	1.0913–1.0955	1.0959	0.428	0.965	0.703	40.5	810
F_{Tree} ($D_{130} < 139$ cm)	-2.682 (0.039)	2.212 (0.015)	1.0923–1.0953	1.0958	0.428	0.966	0.840	40.4	810
$F_{Radiata}$ ($D_{10} < 50$ cm)	-4.858 (0.067)	2.463 (0.027)	1.0259–1.0331	1.0575	0.257	0.972	0.902	21.3	249
$F_{Radiata}$ ($D_{130} < 41$ cm)	-3.740 (0.152)	2.299 (0.058)	1.0272–1.0522	1.0534	0.322	0.915	0.906	26.8	147 [‡]

* Recommended Minimize mean Square Error (MM) correction factor (CF).

† Simple Baskerville correction factor (CF) for reference.

‡ 102 data sets with $D_{130} < 5$ cm excluded in this model.

Table 4

For the seven species that were well sampled ($N > 100$), comparison of prediction performance of lnBGB (*RMSE*, R^2 , *AIC*), and of BGB when back-transformed (*EF* and *MAPE*), following the application of $All_{Universal}$ and the less generalised plant functional type (Table 3) and species-specific models (Table S1). All models applied had, by necessity, D_{10} as the explanatory variable. N indicates the number of individuals to which the models were applied. Note *AIC* can only be compared across categories where N is the same.

Species	Model	N	RMSE	R ²	AIC	EF	MAPE
<i>E. polybractea</i>	$All_{Universal}$	154	0.36	0.56	-114.5	0.59	30.3
	F_{Mallee}	154	0.36	0.87	-304.3	0.57	35.1
	<i>E. polybractea</i>	154	0.36	0.88	-309.2	0.74	30.5
<i>E. loxophleba</i>	$All_{Universal}$	312	0.39	0.65	-101.7	0.80	40.1
	F_{Mallee}	312	0.39	0.91	-532.6	0.93	30.2
	<i>E. loxophleba</i>	312	0.39	0.92	-581.9	0.93	34.5
<i>E. kochii</i>	$All_{Universal}$	114	0.51	0.88	-134.2	0.78	43.8
	$F_{Mallee}^{\#}$	114	0.51	0.82	-83.3	-0.15	100.9
	<i>E. kochii</i>	114	0.51	0.90	-147.3	0.58	47.1
<i>E. globulus</i>	$All_{Universal}$	221	0.33	0.94	-359.4	0.96	76.2
	F_{Tree}	221	0.32	0.96	-450.6	0.98	41.4
	<i>E. globulus</i>	221	0.32	0.97	-502.5	0.99	25.8
<i>E. occidentalis</i>	$All_{Universal}$	114	0.32	0.90	-235.2	0.97	28.9
	F_{Tree}	114	0.32	0.85	-191.0	0.94	26.0
	<i>E. occidentalis</i>	114	0.32	0.91	-251.2	0.99	26.1
<i>P. pinaster</i>	$All_{Universal}$	114	0.41	0.96	-194.7	0.87	51.6
	F_{Tree}	114	0.42	0.96	-187.6	0.84	36.9
	<i>P. pinaster</i>	114	0.41	0.96	-195.7	0.79	38.3
<i>P. radiata</i>	$All_{Universal}$	249	0.28	0.60	-8.72	-0.45	226.0
	$F_{Radiata}$	249	0.26	0.97	-668.8	0.90	21.3

[#] F_{Mallee} model developed for 0.6–81 cm mallee eucalypt trees over-predicted BGB for the 114 relatively small *E. kochii* trees (D_{10} of 1–28 cm); F_{Mallee} application is not recommended for this species until further model validation is possible.

3.4. BGB:AGB

The ratio of BGB:AGB was predicted to differ between the seven unique plant functional types, with the highest values for other low wood density trees and mallee trees and the lowest values for multi-

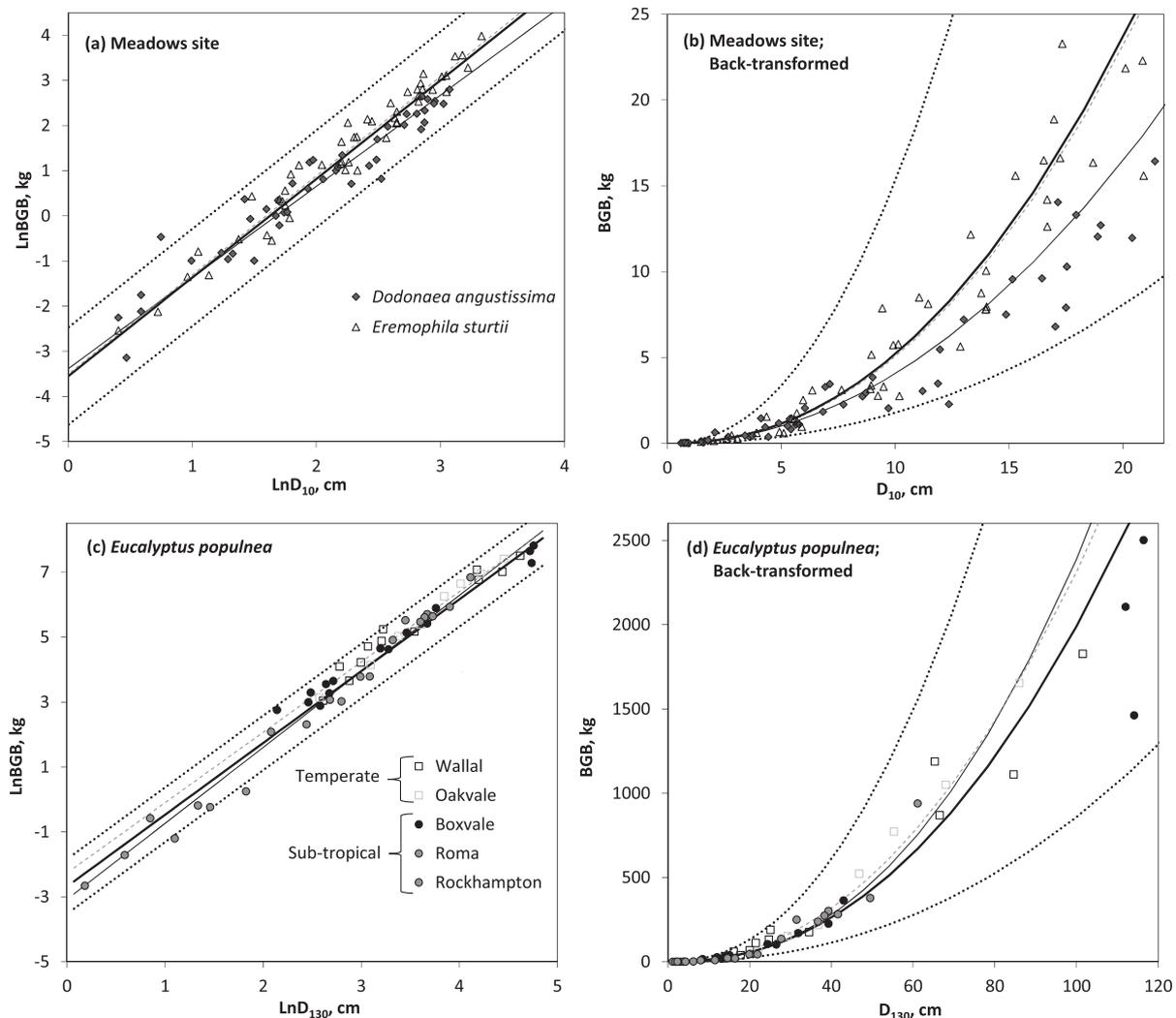


Fig. 5. Application of generic plant functional-type allometric equations for prediction of BGB from stem diameter (D , cm) of (a and b) two species of shrubs sampled at the Meadows site ($F_{Shrub\&Ac}$, D_{10}), and (c and d) the single-stemmed tree species *Eucalyptus populnea* sampled across two different ecoregions (F_{Tree} , D_{130}). Plots (a) and (c) indicate Eq. (2) fitted to the LnBGB data set, and plots (b) and (d) indicate the accuracy of the back-transformed and biased corrected model. Thick black solid lines represent the generic model of best fit, and dotted lines, the 95% prediction interval. The thin black and grey dashed lines represent the model of best fit for the individual species (a and b), or ecoregions (c and d).

stemmed acacias (Fig. 7). With the exception of other high wood density trees, BGB:AGB was predicted to rapidly decline with increasing size of the individual, with equilibrium values attained at $D_{10} > 50$ cm (Fig. 7a, Fig. S3).

The size distribution of individuals sampled will influence the average observed BGB:AGB ratios. Mallee eucalypts tended to have relatively high BGB:AGB, while the softwood species *Pinus radiata* had relatively low BGB:AGB (Fig. 7b). Comparison of the observed and predicted mean (\pm SD) BGB:AGB showed no consistent significant bias in predicted BGB:AGB (Fig. 7b). Due to the high accuracy of the generic allometric models derived for AGB and BGB, predicted BGB:AGB ratios were in agreement (by within ± 0.07) with those observed (Fig. 7b).

4. Discussion

4.1. Allometric models

Results suggest that across a wide range of individuals, BGB can be predicted using generalised plant functional type allometric models with reasonable accuracy and efficiency (72–93%, Fig. 4). Significantly, this is achieved using the easily-measured predictor variable of D .

Although the BGB allometric models were based on datasets covering a broader range of vegetation types and site characteristics than have previously been collated for Australia (including the previously under-represented tropical ecoregions), the fit statistics obtained were comparable to those for generalised allometric models previously developed for much smaller datasets covering smaller stem diameters (Paul et al., 2014). Hence, increasing the domain of application of generalised allometric models does not substantially reduce their prediction accuracy. For example, considering single-stemmed trees with D_{130} 30–45 cm, the average (\pm SD) BGB of 265 ± 89 kg for trees of various genera from tropical moist broadleaf forests (ca 2000 mm yr⁻¹ MAR, $N = 17$, Fig. S4a) was similar to the 266 ± 118 kg found for eucalypt trees from the Mediterranean ecoregion (ca 430 mm yr⁻¹ MAR, $N = 14$, Fig. S4b). Interestingly, although BGB was similar among these individuals of similar size, the area occupied by the root architecture could vary substantially between ecoregions and/or soil types. In our example above, the BGB densities differed between ecoregions (from $3\text{--}7$ kg m⁻³ to $16\text{--}27$ kg m⁻³ soil, respectively, for tropical moist broadleaf forests and sparse stands from Mediterranean ecoregions).

Of the plant functional type models developed, the model for relatively small and heterogeneous multi-stemmed plants ($F_{Shrub\&Ac}$) was

Table 5

Fit statistics from general linear model analysis for assessing whether the allometric model represented by Eq. (2) was improved by the inclusion of site-factors (and their interactions with $\ln D$) as supplementary predictor variables. Factors tested included: (i) binary categorical variable [1,0] of stand age (Age < 20_[1,0]: relatively young at < 20 yrs, or older), (ii) binary categorical variable [1,0] of stand management (Managed_[1,0]: managed or ‘natural’), (iii) categorical variable ecoregion (see Fig. 1), (iv) numerical variable of mean annual temperature (MAT), and (v) numerical variable of mean annual rainfall (MAR). Interactions of these site-factors with $\ln D$ were included in the model only where they were significant. Numbers in parentheses are the number of parameters in the model (C_p values greater than this number indicate models of poor fit). ‘NA’ refers to not applicable, and ‘n.s.’ refers to not statistically significant, with $P < 0.05$. Note; AIC can only be compared across categories where N is the same.

Model	Variables	RMSE	R ²	C _p	AIC
<i>F_{Shrub&Ac}</i> N = 351	$\ln D_{10}$ alone	0.547	0.928	2.00 (2)	-422
	+ Age < 20 _[1,0]	0.503	0.939	4.00 (4)	-478
	+ Managed _[1,0]	0.505	0.939	4.00 (4)	-475
	+ Ecoregion	0.492	0.943	8.00 (8)	-490
	+ MAT	0.537	0.931	4.00 (4)	-431
	+ MAR	0.511	0.937	4.00 (4)	-467
<i>F_{Mallee}</i> N = 644	$\ln D_{10}$ alone	0.469	0.899	2.00 (2)	-972
	+ Age < 20 _[1,0]	0.466	0.900	3.00 (3)	-980
	+ Managed _[1,0]	n.s.	n.s.	n.s.	n.s.
	+ Ecoregion	n.s.	n.s.	n.s.	n.s.
	+ MAT	0.442	0.911	4.00 (4)	-1049
	+ MAR	n.s.	n.s.	n.s.	n.s.
<i>F_{Tree}</i> N = 810	$\ln D_{130}$ alone	0.428	0.965	2.00 (2)	-1372
	+ Age < 20 _[1,0]	0.407	0.969	4.00 (4)	-1451
	+ Managed _[1,0]	0.412	0.968	4.00 (4)	-1433
	+ Ecoregion	0.408	0.969	12.00 (12)	-1423
	+ MAT	0.421	0.967	4.00 (4)	-1399
	+ MAR	0.424	0.966	4.00 (4)	-1386
<i>F_{Radiata}</i> N = 147	$\ln D_{130}$ alone	0.325	0.915	2.00 (2)	-329
	+ Age < 20 _[1,0]	0.275	0.939	3.00 (3)	-377
	+ Managed _[1,0]	NA	NA	NA	NA
	+ Ecoregion	0.266	0.943	4.00 (4)	-385
	+ MAT	0.257	0.947	4.00 (4)	-395
	+ MAR	0.282	0.936	4.00 (4)	-368

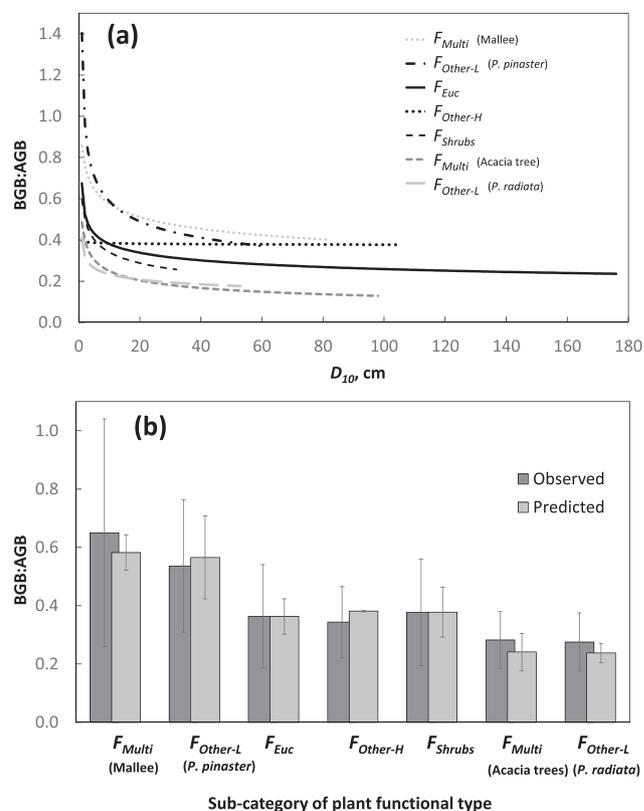


Fig. 7. Predicted BGB:AGB from application of generic allometric equations of BGB and AGB (Paul et al., 2016), in relation to: (a) the size of the individual (D_{10}) for contrasting sub-categories of plant functional types, and (b) the average BGB:AGB observed among contrasting sub-categories of plant functional types. Error bars represent standard deviations.

the least precise, with a relatively high RMSE of 0.545 (Table 3). Measurement of D for small multi-stemmed individuals is prone to relatively high measurement errors (Paul et al., 2017). Further research is currently underway to explore if alternative predictor variables can improve the precision of BGB prediction of such individuals. Further work is also required to explore whether alternative models to the simple power-law model may improve the prediction for BGB across the full range of tree sizes of $F_{Radiata}$, i.e. including trees with $D_{130} < 5.0$ cm.

The data set used was a sub-set of that utilised by Paul et al. (2016) to assess generalised allometry for AGB of trees and shrubs. Performance of the $All_{Universal}$ model for BGB was much poorer than that for AGB (Paul et al., 2016), with the MAPE being 78.9% cf. 40.7%. The $All_{Universal}$ model is therefore relatively inaccurate for BGB prediction, with a higher influence of plant functional type on allometry for BGB than for AGB.

Application of more specific models generally increased the efficiency of prediction of BGB, but only by up to 15–17% (Table 4). This is largely consistent with previous work showing that application of generic multi-species models does not result in loss of accuracy in allometry-predicted AGB compared to species-specific models (Feller 1992; Williams et al., 2005; Montagu et al., 2005; Mugasha et al., 2013; Mbow et al., 2014; Ali et al., 2015; Ishihara et al., 2015; Paul et al., 2016). However, there are exceptions, with biased estimates of BGB for some non-conforming species, which is of concern when applying generalised allometric models to stands dominated by such species. For example, if a woodland is composed of predominately *E. kochii* of moderate size (D_{10} 10–20 cm), and the generic F_{Mallee} model is applied, stand-level BGB estimates are likely to be over-estimated, with bias averaging +6.4 kg per tree (Table 4). Similarly, if a shrubland is composed of predominately *D. viscosa* subsp. *angustissima* of moderate

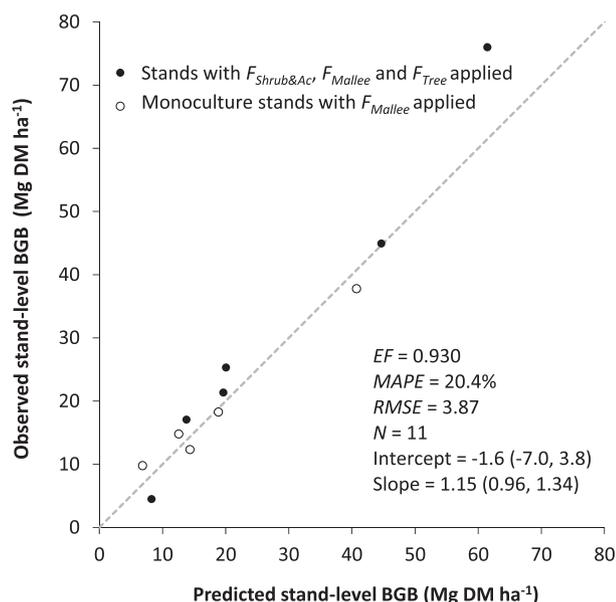


Fig. 6. Relationship between stand-level BGB from whole-plot harvesting at 11 contrasting stands (Table 2) and that predicted for those stands through the application of the generic plant functional type allometric models (Table 3). Values in parentheses are the 95% prediction interval of the slope and intercept. Grey dashed line represents the 1:1 line.

size (D_{10} 10–20 cm), and the generic $F_{Shrub\&Ac}$ model is applied, stand-level BGB estimates are likely to be over-estimated, with bias averaging +2.3 kg per tree (Fig. 5b).

Further research is required to ensure there is negligible bias in prediction of BGB for specific species represented by each plant functional type (Paul et al., 2018b). Only seven species were sampled sufficiently to verify this. Based on the findings of Roxburgh et al. (2015), an N of ca 50–110 individuals will be required to ascertain the true allometry of a given species, i.e. to achieve a coefficient of variation of BGB prediction of 5%. Even assuming consistency in the protocols used to excavate roots, a larger inherent variability (and hence, larger required sample size) of BGB cf. AGB allometry is to be expected. Indeed due to the difficulty in sampling BGB, uncertainty associated with measurement errors of BGB average about $\pm 16\%$ (Paul et al., 2014). Furthermore, BGB allometry may be influenced by factors such as the presence of substantial root suckering, and the degree of senescence in response to recent disturbance, e.g. fire, grazing. In the example shown in Fig. 5b, BGB allometry of *E. sturtii* may be related to this species' ability to form extensive colonies via root suckers, whereas BGB allometry of the relatively fire- and grazing-sensitive *D. viscosa* subsp. *angustissima* may be influenced by disturbance-induced cycles of senescence and re-shooting (NSW LLS, 2014).

4.2. Inclusion of stand- or site-factor predictor variables

Including stand (age, management) and climate (MAR, MAT) characteristics as predictor variables, even where statistically significant, did not markedly improve the predictive ability of D -based models, with increases in R^2 of < 3% (Table 5). Even when the same species was reasonably-well sampled across contrasting ecoregions, negligible differences in BGB allometry were observed (Fig. 5d). For a given species and size range, within-site variation is often as great as between-site variation in BGB. Thus there is only a minor trade-off in accuracy from application of simple power-law models based on D -alone relative to more complex models that include multiple explanatory variables (Sileshi, 2014; Picard et al., 2015; Paul et al., 2016).

Recent analysis of a global biomass data set which combined our data set (Table 1) with similar data sets from other continents (Ledo et al., 2018), showed that after D , the next most important factor influencing allometry (in this case, of BGB:AGB) was the deficit between monthly rainfall and potential evapotranspiration. BGB:AGB increased with increasing moisture deficit, which accounted for 17% of the variance in BGB:AGB. Although BGB:AGB differed between different vegetation types, due to a correlation between vegetation type and climate, when the moisture deficit was accounted for, the vegetation type ceased to be an important explanatory variable (Ledo et al., 2018).

In the present study, climate factors appeared to be inherently accounted for in the grouping of species into plant functional types. The inclusion of plant functional types greatly improved the performance of the $All_{Universal}$ models for Australian trees and shrubs (Fig. S1, Table 4), yet the inclusion of climate factors had marginal impact (Table 5). Clearly, plant functional attributes often reflect coordinated adaptations to environmental factors (Onoda et al., 2010; van Gelder et al., 2006; Banin et al., 2012; Pfautsch et al., 2016), and such convergence probably also accounts for differences in allometry between plant functional types.

Despite plant functional types inherently accounting for some climate-related factors, for each of the four plant functional types, the inclusion of ecoregion, MAR and/or MAT as explanatory variables resulted in some (although minor) improvement to predictive performance, with this being greater for BGB (Table 5) than for AGB (Paul et al., 2016). It remains unclear whether the effect of such climate variables would have been greater on BGB allometry of plant functional types had our data set encompassed an even greater range of the ecoregions. A next step is to evaluate the impact of climate, and hence climate change, on BGB allometry through measurement of more

individuals from the relatively under-sampled combinations of various plant functional types and ecoregions from different regions of the world (e.g. tropical and subtropical regions, medium to high rainfall, tall closed temperate forests, and arid shrublands, Fig. 2). Additional data may also facilitate the assessment of more subtle influences (e.g. soil type and topography) on BGB allometry.

Our assessment of the impacts of stand age and management on BGB allometry included only broad categories of managed or unmanaged, and younger or older than 20 years. This was a necessity given insufficient observations in the data set to explore whether, across a range of plant functional types and ecoregions, BGB allometry changes with age, stand structure and management. Although relatively localised and species-specific studies of BGB have explored some of these factors (e.g. Ritson and Sochacki, 2003), further work is required to confirm their significance more broadly.

4.3. Model validation at the stand-level using whole plot root excavation

Application of allometric models based on plant functional type resulted in high efficiency of prediction of stand-level BGB across contrasting direct-measurement stands (Fig. 6). Previously, Paul et al. (2014) used these same whole-plot excavation data to validate BGB allometric models developed using BGB of individuals covering a smaller range of sizes, and sampled from mixed-species environmental and mallee plantings. Despite the fact that allometric models developed in this study included a broader range of vegetation types and site characteristics compared to those developed by Paul et al. (2014), the decline in efficiency of BGB prediction across these 11 direct stands was only 6%. This provides further evidence that increased applicability of allometric models does not result in significant loss of accuracy.

Application of species-specific models resulted in only a modest improvement in the efficiency of prediction of stand-level BGB compared to the application of more generalised models based on plant functional types (Fig. S1 cf. Fig. 6). Furthermore, for mixed-species stands, due to the smaller sample size and larger overall number of model coefficients to parameterise, uncertainties associated with the propagation of errors (including measurement, model-fitting and prediction errors) may be larger following application of multiple species-specific models compared to a single generalised multi-species model. Additionally, large sample sizes are required for each species-specific model (Roxburgh et al., 2015), resulting in significant costs associated with development of models for each new species. These likely higher uncertainties and costs would negate the small gain in average accuracy of stand-level BGB prediction when applying multiple species-specific models versus a generalised multi-species model in mixed-species stands. Models generalised at the level of plant functional group (Eqs. (3a)–(3d)), reported using the Baskerville CF) are recommended for application in both Australia, and for validation in similar ecoregions in other parts of the world.

BGB (kg) for species of:

$$F_{Shrub\&Ac} = \exp[-3.553 + 2.185 \ln D_{10}] \times 1.160 \quad (3a)$$

$$F_{Mallee} = \exp[-2.946 + 2.302 \ln D_{10}] \times 1.116 \quad (3b)$$

$$F_{Tree} = \exp[-2.682 + 2.212 \ln D_{130}] \times 1.096 \quad (3c)$$

$$F_{Radiata} = \exp[-3.740 + 2.299 \ln D_{130}] \times 1.053 \quad (3d)$$

As with all allometric models, to avoid bias in BGB predictions, recommended models should only be applied within their valid diameter range as indicated by the maximum D sampled (e.g. Tables 3 and S1). There are two exceptions to the recommendation of application of Eq. (3) for stand-level prediction. First, where the trade-off between accuracy and cost effectiveness is relatively high, e.g. for a given high-biomass stand comprising only one or two dominant species. In such instances, additional costs associated with obtaining species-specific models may warrant the improved accuracy. Second, where BGB

estimates are required for stands dominated by species suspected of not conforming to the generalised plant functional groups models (e.g. poor representation of *E. kochii* by the F_{Mallee} model, and *D. viscosa* subsp. *angustissima* by the $F_{Shrub&Ac}$ model, respectively). Recommended statistical approaches are provided by Paul et al. (2018b).

4.4. BGB:AGB

As outlined earlier, estimates of BGB based on *D* are preferable to those based on a ratio to AGB, particularly when estimates of AGB are only available at the stand-level. Indeed, predictions of BGB:AGB were relatively uncertain as they include the uncertainty in both allometry-predicted BGB and AGB (Fig. 7b, Fig. S3). Nonetheless, the results are of interest in demonstrating how BGB:AGB of Australian woody plants vary with size and functional type. As expected, predictions of BGB:AGB decreased with increasing *D* (Fig. 7a). This is consistent with the understanding that saplings invest more biomass below ground for nutrient and water acquisition to facilitate rapid early growth and survival, and with non-conductive xylem accumulating in AGB as *D* increases (Barton and Montagu, 2006; Poorter et al., 2012). Further, BGB:AGB estimates were relatively high for mallee species that have lignotubers and have evolved in relatively arid environments (Paul et al., 2014), but relatively small for *P. radiata* trees that are established in fast-growing and fertilised plantations, with presumably relatively little investment BGB allocation (Ledo et al., 2018).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.08.043>.

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