Allometric Estimates of Aboveground Biomass Using Cover and Height Are Improved by Increasing Specificity of Plant Functional Groups in Eastern Australian Rangelands[☆]

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A B S T R A C T

Plant aboveground biomass (AGB) is a useful metric to assess ecosystem functioning, and its sensitivity to changing environmental conditions provides insight into potential global change impacts. Allometric estimates of AGB using vegetation characteristics such as plant cover or height provide nondestructive biomass proxies for repeated measurements but can introduce uncertainty to estimates. We estimated the relationship between both plant *cover* and a *cover·height index* and AGB for 15 plant species from six sites to identify the most reliable approach to estimate biomass nondestructively in semiarid eastern Australian rangelands. Estimates were made by grouping species at four different levels of specificity, to test whether generic estimates were more robust than grouping species based on life history and morphological characteristics. Estimates were then tested on a 1.5-m^2 plot at each site for validation. In all cases, models were highly significant ($P < 0.001$) with adjusted R^2 values ranging from 0.42 to 0.96 for *cover* models and 0.38 to 0.98 for *cover·height index* models. We found the addition of *height* improved model fits in four groups while reducing model fits in two groups. The error around AGB estimates for *cover·height index*−based models ranged from −66.8 to 4% (absolute mean 35%). *Cover*-based models had errors between −13.4% and 53% (absolute mean 14.2%). For *cover*-based estimates of AGB in validation plots, grouping plants by plant functional types (PFTs) increased accuracy (absolute mean error 17.3%) compared with estimates using data from all 15 species (absolute mean of 65.2%). Overall cover was a useful surrogate to estimate AGB (with the exception of one site, accuracy ranged from −2.3% to 11.5%), while height (thought to be a surrogate for canopy characteristics) provided benefit in a few circumstances. We suggest that future research should test additional nondestructive proxies and group species based on PFTs to improve AGB estimates using allometry.

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Introduction

Robust measurements of aboveground net primary productivity (ANPP, g m^{-2} yr^{-1}) are critical for monitoring ecosystem sensitivity to climatic variability (Knapp and Smith 2001; Scurlock et al. 2002) and calculating landscape-level carbon stocks or global carbon dynamics (Le Quéré et al. 2015). In many plant communities, the use of destructive sampling to obtain ANPP data can result in permanent loss of harvested individuals with substantial

consequences for the ecology of the system (Guevara et al. 2002; Flombaum and Sala 2007; Montès 2009). Destructive sampling is also time-consuming and costly, and especially in remote locations, there are challenges to transporting and processing large amounts of material. The strategy for estimating AGB can vary depending on the plant community and factors regulating productivity (Sala et al. 1988; Biondini et al. 1991). For example, grasslands typically undergo destructive harvests at either peak biomass or several times throughout the year (seasonal peak biomass) (Singh et al. 1975; Sala et al. 2000). Repeating these measurements over time may alter species composition by selecting plants that are not affected by clipping (e.g., perennial grasses) rather than those that are impacted negatively (e.g., shrubs). In Australia, where rainfall is expected to become more variable, estimates of changes in AGB will become increasingly important to quantify global carbon dynamics (New et al. 2001; Haverd et al. 2016). In addition, economic output

is dependent on vast rangelands and grazing management (Bird et al. 1992; McAlpine et al. 2009). Developing sound methodologies to rapidly quantify AGB in shrub and herbaceous-dominated plant communities and determine how it changes in response to altered rainfall patterns and climate more generally is crucial.

The development of allometric estimates of AGB is underpinned by two key decisions (Paul et al. 2016). The first is to determine which predictor variables (or plant attributes) are most likely to correlate with standing AGB. In forests, the established paradigm of using stem diameter, stem height, and wood density has proven accurate in predicting AGB (Picard et al. 2012; Chave et al. 2014; Picard et al. 2015). In contrast, cover-based and volumetric methods are widely used for predicting AGB in grass- and shrub-dominated ecosystems (Huenneke et al. 2001; Flombaum and Sala 2007; Nafus et al. 2009). The cover-based method uses linear regression to determine the relationship between vegetation cover (x-axis) and standing AGB (y-axis), where the intercept is typically set to zero (i.e., no cover equals no biomass). However, obtaining a sufficient number of data points along the vegetation cover axis may require removal of portions of a plant to obtain the required "spread" (i.e., to include low values), which may increase uncertainty in estimates (Montès 2009). The volumetric method uses linear regression to estimate AGB (y-axis) from volume data derived by multiplying cover by height (x-axis). The calculated volume does not represent the individual plant but rather a three-dimensional shape in which the plant is hypothetically encased. The slope of the linear relationship between AGB (y-axis) and either volume (x-axis) or cover (x-axis) can then be used to nondestructively estimate AGB at a given site using *cover* only or *cover·height index.*

Several studies have used cover, sometimes in combination with height, to estimate the impact of year-of-sampling or location on the measurement-AGB relationship. For example, in a semiarid herbaceous system in central Hungary (mean annual precipitation of ~500 mm), the relationships between visually estimated plant cover and AGB varied between years and was increasingly positive (greater AGB per unit cover) with greater amounts of rainfall preceding harvests (Ónodi et al. 2017); however, the authors did not use height in their estimates. Others have found the addition of height did not significantly improve AGB estimates in grass-based communities (Andariese and Covington 1986; Assaeed 1997; Guevara et al. 2002; Nafus et al. 2009). Since above-average rainfall can result in greater AGB production and associated increases in light-limitation (Knapp 1984), the inclusion of height may be beneficial and provide a mechanistic link for developing robust allometric estimates to be used in longitudinal studies within herbaceous plant communities, even if height does not aid in AGB estimates at a single time point. In addition, plant height may be indicative of competitive vigor (Cornelissen et al. 2003), which is likely to vary given environmental heterogeneity (Menaut and Walker 2001). The natural variation in height found in a plant community may provide a sufficient "spread" along the x-axis for robust regression analysis of plant attribute-AGB relationships.

The second key decision is to determine the level of specificity (e.g., species, genus, functional group) required to develop robust allometric estimates (Paul et al. 2016). In other words, are plant attribute-AGB relationships for every species required or can plant species of similar form, habitat and/or life history traits be grouped? Paul et al. (2016) tested this concept in Australia using 274 woody plant species (trees and shrubs) across 826 sites and concluded generalized allometric equations did not present substantial bias or inaccuracy in predicting AGB. This result suggests that the way species are grouped and their home ecoregion is possibly arbitrary for estimating AGB. Similarly, Nafus et al. (2009) found that multispecies allometric estimates (using basal diameter and height) of eight grass species were robust in the semidesert rangelands of Arizona. However, unlike Paul et al. (2016), Nafus

et al. (2009) cautioned against using the biomass-size relationships at other sites because intersite variation in allometric relationships has been observed across broad plant functional groups (e.g., deciduous trees, shrubs, grasses) (Andariese 1986; Buech and Rugg 1989; Ares and Fownes 2000). In arid and semiarid herbaceous communities (e.g., grasslands), pulse-rainfall patterns may result in periods where communities fluctuate between being water limited (light abundant) and light limited (water abundant), thereby leading to changes in vegetation height (i.e., greater plant height with increasing light limitation) (Knapp 1984). If so, the addition of height to allometric estimates may permit cross-site use of allometric estimates of AGB.

A common theme among allometric studies has been the potential trade-off between species-specific and multispecies estimates (Fig. 1) and determination of species groupings (Nafus et al. 2009; Conti et al. 2013; Fayolle et al. 2013; Paul et al. 2016). Coarse characteristics of plant groups (woody vs. herbaceous, shrub vs. grass) may be ideal to address this issue as assignment and classification of plants in the field would be rapid. Communities can be described as being composed of forbs, grasses, shrubs, and trees. A key issue for ecologists in the field is therefore how to optimize the use of species groupings in the determination of biomass allometry relationships. Ishihara et al. (2015) investigated this topic and found generic equations (i.e., equations across groupings) were sufficient in predicting AGB in a Japanese forest, even when the plant attribute−AGB relationships were developed off site. They found broad plant groups (deciduous, evergreen, angiosperm, gymnosperm) were useful. These criteria, however, fail to capture the physical structure of grass- and forb-dominated communities, indicating that unique levels of specificity and plant groupings are required for allometry in herbaceous systems, depending on the habitat type and resolution of interest.
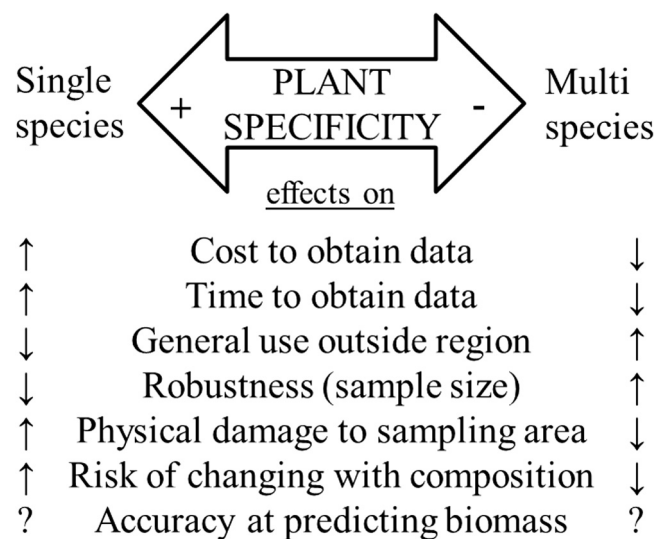
Figure 1. A summary of how specificity of plant groupings represents trade-offs for generating allometric estimates of biomass. Single species (high specificity) and multispecies (low specificity) allometric estimates logically have trade-offs. Arrows indicate how each performance criteria might change with plant specificity. Developing allometric estimates for individual species can increase cost and time to obtain data. In addition, the use of these estimates outside the collected region (i.e. off-site usage) may be limited and the overall number of samples obtained (robustness) will be restricted. Individual species estimates, therefore, will require a greater number of samples, resulting in greater damage to the sampling area. In addition, if a species no longer exists at that site over time (say through the implementation of a treatment) there is a chance that the allometric equation will no longer be useful. Less is known about how species-specific and multispecies allometric estimates compare at accurately predicting actual biomass.

Table 1
Sites, locations, and rainfall characteristics. Sites are paired by mean annual precipitation but vary in interannual variation (CV = mean/standard error).

Site name (and state)	Coordinates	Mean annual precipitation (mm)	Coefficient of variation (CV)	Standing biomass (g·m^2)[1]
Broken Hill, NSW	31°58'33.2"S, 141°33'19.3"E	251	0.28	215.0
Milparinka, NSW	29°36'21.2"S, 141°43'01.9"E	265	0.52	268.5
Cobar, NSW	31°47'45.0"S, 145°35'46.7"E	367	0.27	397.1
Quilpie, QLD	26°34'38.1"S, 144°37'08.5"E	356	0.57	147.1
Nyngan, NSW	31°38'42.7"S, 146°38'30.8"E	466	0.31	523.1
Charleville, QLD	26°21'53.1"S, 146°09'02.6"E	442	0.53	275.3

Precipitation data from the Bureau of Meteorology (http://bom.gov.au), averaged from 2002 to 2012.
[1] Data obtained from "validation plots" located outside the permanent plot area.

The aim of this project was to develop a simple and rapid methodology to estimate AGB across eastern Australian rangelands using broad plant functional groups (herein categories). More specifically, we wanted to 1) determine if the addition of height (using *cover·height index*) improved AGB estimates relative to using *cover* alone; 2) determine the optimum level of specificity for plant groupings that maximizes the accuracy of allometric estimates of AGB; and 3) investigate if the accuracy (percent error) in estimated ABG biomass was similar across each of the six sites used for plant collection. We hypothesized that the addition of height would improve estimates of AGB across all levels of specificity since "height" and "functional group" are likely to be related, both being indicative of plant strategy. In addition, we hypothesized that the accuracy of AGB estimates would be highest when using more specific plant categories. Lastly, we hypothesized that the accuracy of the allometric estimates (tested against destructively harvested validation plots) would vary across sites because of differences in species diversity and abundance at each site.

Materials and Methods

Sites and Species Selection

Six field sites were selected as part of the ecological research project "Dryland Rainfall Legacies" (DRL) investigating the effect of historic rainfall patterns on ecosystem sensitivity to rainfall variability, established in September 2016. The six sites vary in 10-yr annual rainfall amounts and in their interannual variability in rainfall over that period (Table 1). Nine permanent vegetation plots (1.5 m^2 each) were surveyed for plant cover using the Daubenmire method (Daubenmire 1959) with a gridded quadrat (1.5 m^2) at each site (54 plots total). Plant species for allometric calculations were selected on the basis of the most abundant species at that site and the availability of individual plants outside the permanent plots.

Data Collection

Based on vegetation surveys and availability of plant material, 15 species were selected for this study and biomass data were collected in September 2016 (experiment initiation, beginning of spring) and March 2017 (end of summer) (Table 2). Data were grouped into three categories on the basis of observations in the field and species information in the literature (Cunningham et al. 1992). Category A is the broadest, distinguishing two groups: *herbaceous* (12 species) and *woody* (3 species). Category B uses phylogeny and primary growth form to distinguish three groups: *forbs* (8 species), *grasses* (4 species), and *woody shrubs* (3 species). Category C is the most specific with six groups: *leafy woody shrubs* (one species); *sclerophyllous woody shrubs* (two species); *forbs* (three species); *subshrubs* (four species); *long-lived grasses* (two to three species, see later); and *short-lived grasses* (2 species). *Subshrubs,* or bushes, were considered to be plants that may have woody components (particularly at the base), but where the

majority of growth (stems and branches) is herbaceous (Jackson 1905). *Long-lived* and *short-lived* grasses were determined on the basis of the presence of a "crown" when foliar die-back occurred in drier periods. All four grass species sampled are perennial; the persistence of a crown indicates that it is the same individual "regrowing" when rainfall occurs following a dry period (Cunningham et al. 1992). Long-lived grasses, *Astrebla lappaceae, A. pectinate,* and *Eragrostis setifolia,* were found to have persistent crowns during the second sampling in March 2017, while the remaining two species did not. Both *Astrebla* species were combined for analyses because they have nearly identical growth forms (Cunningham et al. 1992) and are found at the same site (Milparinka).

Cover and *height* data were collected for each individual plant within the validation plots. Plots often had numerous small-statured individuals of the same species, so we counted (estimated by area in some cases) the number of individuals and calculated an average *cover* value by dividing the total *cover* value by the number of individuals. In addition, *height* was estimated for ~5 individuals and the average value was used for all individuals of that species. For species and individuals that contributed a greater amount to total *cover* estimates (> 3% per individual), *cover* and *height* were collected for each individual plant. *Height* was measured as the stretched length to the tallest nonreproductive point. The *cover* (m^2) and *cover·height index* (m^3) of each plant were used to estimate AGB. The whole aboveground portion of the plant was harvested using hand-pruners and stored in paper bags. Samples were subsequently dried at 60°C for 72 h and weighed. At each site, one "validation plot" (1.5 m^2) (see Table 1) was used for subsequent "accuracy" testing of the allometric estimates based on data collected from the individual plants. Each validation plot was assessed for cover (Daubenmire 1959), measured for vegetative height using the tallest individual of each species, and then harvested in its entirety to ground level. The AGB$_{Validation}$ was sorted out by species, dried, and weighed separately. *Cover* and *cover·height index* data were presented in the units of m^2 and m^3, respectively.

Data Analysis

Data for creating *cover*-AGB and *cover·height index*−AGB estimates were analyzed with linear regression in R (R Studio V1.0.143, R V3.2.5, R Core Team 2013) using the *"lm"* function. The scatterplots for linear assumptions are presented in Supplementary Figures 1 and 2 for *cover* and Supplementary Figures 3 and 4 for *cover·height index.* The intercept of the linear model was set to zero, because zero plant cover would equal zero AGB, and each species included a "0 cover/cover·height index and 0 AGB" data point to reflect this (Flombaum and Sala 2007). Data were not transformed. Alpha was set at 0.05. This equation was calculated for 1) total species (i.e., all species data combined); 2) category A (2 groups); 3) category B (3 groups); and 4) category C (6 groups), as well as for species-specific data. Species-specific data were unavailable for

Table 2
Details for collected species including sample size *(n)* and categories (A = broadest, B = intermediate; C = most specific). "Range of cover values" indicates the size of individuals that were used to develop allometric estimates.

Species	Family	N	Site	Collected	Category A	Category B	Category C	Range of cover values [min-max] (cm^2)
Astrebla lappaceae (Lindl.) Domin; *A. pectinata* (Lindl.) F. Muell. *ex* Benth.	Poaceae	40	Milparinka, NSW	March 2017	Herbaceous	Grass	Long-life grass	24-3 240
Eragrostis setifolia Nees.	Poaceae	30	Quilpie, QLD	March 2017	Herbaceous	Grass	Long-life grass	25-696
Austrostipa scabra (Lindley) S.W. Jacobs & J. Everett	Poaceae	10	Nyngan, NSW	March 2017	Herbaceous	Grass	Short-life grass	4-400
Thyridolepis mitchelliana (Nees) S. T. Blake	Poaceae	30	Nyngan, NSW	March 2017	Herbaceous	Grass	Short-life grass	1-64
Calotis lappulacea Benth.	Asteraceae	30	Nyngan, NSW	March 2017	Herbaceous	Forb	Forb	6-810
Ptilotus sessilifolius (Lindl.) Benl	Amaranthaceae	30	Cobar, NSW	March 2017	Herbaceous	Forb	Forb	8-713
Rhodanthe floribunda (A.Cunn. *ex* DC) Paul G. Wilson	Asteraceae	25	Milparinka, NSW	March 2017	Herbaceous	Forb	Forb	20-840
Abutilon halophilim F.Muell.	Malvaceae	15	Milparinka, NSW	March 2017	Herbaceous	Forb	Subshrub	418-3 480
Atriplex vesicaria Heward(es; fr) ex Benth.	Amaranthaceae	20	Broken Hill, NSW	September 2017	Herbaceous	Forb	Subshrub	144-1 215
Sclerolaena eriacantha (F. Muell.) Ulbr.	Chenopodiaceae	25	Quilpie, QLD	March 2017	Herbaceous	Forb	Subshrub	25-486
Sclerolaena ventricosa (J.M. Black) A.J.Scott	Chenopodiaceae	15	Broken Hill, NSW	September 2017	Herbaceous	Forb	Subshrub	135-897
Sida petrophila F. Muell.	Malvaceae	20	Broken Hill, NSW	March 2017	Herbaceous	Forb	Subshrub	1-676
Eremophila gilesii F. Muell.	Scrophulariaceae	30	Charleville, QLD	March 2017	Woody	Shrub	Leafy	462-9 800
Maireana pyramidata (Benth.) Paul G. Wilson	Chenopodiaceae	15	Broken Hill, NSW	March 2017	Woody	Shrub	Sclerophyllous	228-7 875
Maireana sedifolia (F. Muell) Paul G. Wilson	Chenopodiaceae	15	Broken Hill, NSW	September 2017	Woody	Shrub	Sclerophyllous	104-2 332

most specific analysis, so these used a combination of species-specific data (when available) to estimate AGB and, if unavailable, category C data (i.e., the next most specific) were used to estimate AGB. Model selection was based on comparison of adjusted R^2 values, Akaike's information criterion (AIC), and root mean square error (RMSE). Models with lower AIC were considered better estimates. The rules we applied regarding the use of AIC for model selection were that 1) models with a difference of < 2 should both be considered for selection; and 2) models with a difference of > 10 should be omitted (in preference of the lowest AIC) (Burnham and Anderson 2002). Models with a difference in AIC between 2 and 8 are not significantly different and should be chosen on the basis of intended usage (Akaike, 1992).

The percent change ([*cover-index*]/[*cover*] · 100) was calculated for the adjusted R^2 and RMSE. In other words, a positive percent change would indicate that the addition of height increased the adjusted R^2 or RMSE. It is important to note that increased adjusted R^2 means greater amounts of variation were explained by the model and increased RMSE means less variation was explained by the model. Improvement in AIC was calculated as the *cover* AIC minus the *cover·height index* AIC, meaning a positive value indicates that adding height improved AGB estimates. In all cases there was only one predictor value (*cover* or the volume from the *cover·height index*), which would not introduce bias to adjusted R^2 or AIC values. Adjusted R^2 is comparable across prediction parameters and is commonly used for allometric estimates of AGB. The use of AIC to select allometric models is well established (Burnham and Anderson 2002). Reporting RMSE is common and represents a biologically relevant approach to compare allometric equations. For example, if the *cover*-AGB relationship estimate is 500 g·m^2, with a RMSE term of 50 g·m^2, we could say that 50% plant *cover* would be 250 ± 50 g·m^2 of AGB. The ratio of RMSE to the slope is useful because it allows comparison across groups with unique slopes and error terms. For example, a RMSE of 50 with a slope of 100 (50/100 = 50% of the estimated value) would be superior to a RMSE of 10 if the slope is 16 (10/16 = 62.5% of the estimated value). All three metrics were used to determine whether height (i.e., *cover·height index*) improved allometric estimates of AGB. Adjusted R^2 and

RMSE were considered as a % increase (better) or % decrease (worse) without a threshold to determine whether the % change was "significant."

Slopes (change in AGB per unit *cover* or *cover·height index*) were used to estimate AGB using cover and height data obtained from the validation plots. This was done using the "total species" and category-based equations for both *cover* and *cover·height index* values. The accuracy of predicted (i.e., model-based) AGB data was determined by comparison with data from all validation plots. The percent error was calculated by dividing the difference between AGB$_{Observed}$ and AGB$_{Predicted}$ by the AGB$_{Observed}$ value. This was calculated using validation plots from each site individual, as well as the pooled data from six plots (one plot per site).

The question of how to select the most appropriate equation or model fit remains a key issue when conducting allometric estimates of biomass across multiple taxa and lifeforms (Chave et al. 2004; Chen et al. 2009; Zhu et al. 2009; Molto et al. 2013). Several different approaches have been reported in the recent literature. For example, Chave et al. (2014) used bioclimatic predictors of AGB that led to the lowest residual standard error (RSE) while previously reporting RSE and AIC in estimates of AGB in a tropical forest (Chave et al. 2005). For high-elevation grassland plant species, Oliveras et al. (2014) reported adjusted R^2, RMSE, and AIC. In a broader allometric assessment of AGB of trees, shrubs, and herbaceous plants, Ensslin et al. (2015) selected proxy-AGB fits based on AIC but still reported adjusted R^2. For the purpose of this study, we chose to report AIC, adjusted R^2, and RMSE.

Results

Overall Model Fit Summary

All regression results were highly significant ($P < 0.001$) with adjusted R^2 values ranging between 0.38 and 0.98. The slope for total species combined using cover was 830 g·m^2 (Table 3), while *cover·height index* was 1 556.7 g·m^3 (Table 4). Using Category A, there was a small difference in the *cover·height index* estimate

Table 3
Slopes, adjusted R^2, root square mean errors (RMSE), the RMSE/slope ratio, and Akaike's information criteria (AIC) for plant categories and species tested for *cover*-aboveground biomass relationships. All relationships are highly significant ($P < 0.001$).

Category/Binomial	Slope (g·m²)	Adjusted R^2	RMSE (g·m²)	RMSE/Slope	AIC
All species	830.0	0.58	96.6	0.116	4 616.1
Category A					
Woody	863.5	0.57	234.8	0.272	870.8
Herbaceous	590.0	0.83	13.9	0.024	2 612.7
Category B					
Forb	549.5	0.81	14.0	0.026	1 531.0
Grass	649.9	0.87	13.1	0.020	1 073.7
Shrub	863.5	0.57	234.8	0.272	870.8
Category C					
Forb	594.5	0.68	12.0	0.020	1 018.3
Subshrub	537.4	0.87	17.7	0.033	502.2
Leafy shrub	528.1	0.76	116.7	0.221	387.5
Sclerophyllous shrub	2 106.3	0.94	111.3	0.053	396.8
Long-life grass	650.4	0.88	17.0	0.026	616.1
Short-life grass	606.7	0.42	6.1	0.010	403.5
Species specific					
Maireana pyramidata	2 076.4	0.96	113.4	0.055	201.7
Atriplex vesicaria	726.5	0.95	10.1	0.014	161.4
Sclerolaena ventricosa	964.3	0.90	16.9	0.018	140.9
Ptilotus sessilifolius	390.5	0.81	4.3	0.011	182.6
Abutilon halophilim	500.5	0.86	27.6	0.055	156.5
Astrebla lappaceae & A. pectinata	661.9	0.88	21.4	0.032	371.8
Thyridolepis mitchelliana	2 350.5	0.54	5.0	0.002	191.7
Eragrostis setifolia	520.1	0.84	6.8	0.013	211.0
Maireana sedifolia	2 360.7	0.80	106.2	0.045	199.6
Sida petrophila	386.2	0.92	3.2	0.008	113.2
Austrostipa scabra	566.9	0.84	3.6	0.006	65.0
Sclerolaena eriacantha	646.2	0.90	3.6	0.006	114.3
Eremophila gilesii	528.1	0.76	116.7	0.221	387.5
Rhodanthe floribunda	382.4	0.81	4.0	0.010	150.4
Calotis lappulacea	228.0	0.57	6.0	0.026	203.3

between woody and herbaceous species (1 562.0 g·m³ and 1 472.3 g·m³, respectively), while the estimates diverged using *cover* only (863.5 g·m² and 590 g·m², respectively).

Within Category B, the relationship between AGB and *cover* indicated that the greatest AGB·m² was for *shrubs* (863.5 g·m²) and the lowest AGB·m² was for *forbs* (549.5 g·m²). The *cover·height index* indicated that *grasses* had the lowest AGB·m³ (1 314.0 g·m³) and *forbs* had the highest (1 740.2 g·m³).

Cover-only data for Category C groupings resulted in five of the six plant types having AGB/area slopes between 528.1 g·m² and 650.4 g·m². The exception, *Sclerophyllous shrubs,* had greater than 3× the AGB for the same area. Using *cover·height index* gave similar results, in that the slope for *sclerophyllous shrubs* was 1 466.3 g·m³ greater than the second largest group in Category C (2365.2 g·m³ for *short-life grasses*) and even greater than the remaining groups; however, there was noticeably greater range in values compared with *cover*-based estimates overall.

Model Fit Improvement with Addition of Height

Changes in adjusted R^2, AIC, and RMSE are reported in Table 5. A positive change in adjusted R^2 indicates a model improvement with the addition of height. A positive change in RMSE indicates the error term increased with the addition of height, indicating a less robust model fit. Using *cover·height index* rather than *cover* improved regression equations in 4 out of 12 instances; however, there were 2 cases where the addition of height reduced the model fit. Changes in adjusted R^2, AIC, and RMSE were independent of one another. For example, the largest improvement in adjusted R^2 (11.0%) and RMSE (−19.3%) occurred in Category C *leafy shrubs* while the largest improvement in AIC (21.3 unitless) occurred when adding height to the "total species" estimate. Adding height had the least effect on Category C *subshrubs* based on adjusted R^2 and RMSE and on category A *herbaceous* plants based on AIC.

Accuracy of Allometric Estimates in Validation Plots

Standing biomass (from validation plots) errors are presented in Figure 2, for *cover*- and *cover·height index*−based allometric equations. Generally, increasing specificity of plant groups improved AGB estimates compared with estimates using total species combined *cover*-based estimates; however, the AGB prediction accuracy varied between sites with increasing specificity using. In Cobar and Broken Hill, intermediate specificity of plant groups (CatB) yielded the most accurate AGB prediction (see Fig. 2c), while CatA was the best in Milparinka (see Fig. 2b). In the three remaining sites, however, either CatC or a combination of species-specific data (with CatC for those species without species-specific data) yielded the most accurate predictions (see Fig. 2d and 2e, respectively). In the case of Charleville, there was no difference between *cover*-based AGB estimates in CatC and species-specific data, likely because the majority of AGB in the validation plot was from *Eremophila gilesii*. With the exception of Quilpie, the accuracy of *cover*-based predictions of AGB ranged from −2.3% to 11.5%, indicating *cover* as a useful proxy of AGB for most sites.

Unlike *cover, cover·height index*−based estimates were not necessarily improved by increasing specificity of plant groups. At the three northern sites, the generic "total species" equation was the superior predictor of AGB; however, increasing specificity improved estimates at the southern sites (see Fig. 2a). Generally, *cover·height index*−based estimates were inferior to cover having an error range of −66.8% to 4%. A potential exception would be Quilpie, where the superior *index*-based estimate ("total species" equation) had an error of −5.0% while the *cover*-based estimate (species-specific equation) had an error of 53%.

Discussion

In this study, we sought to 1) test whether allometric estimates of AGB using *cover* can be improved by adding height

Table 4
Slopes, adjusted R^2, root mean square error (RMSE), the RMSE/slope ratio, and Akaike's information criteria (AIC) for categories and species tested for *cover·height index*–AGB relationships. All relationships are highly significant ($P < 0.001$).

Category/Binomial	Slope (g·m³)	Adjusted R^2	RMSE (g·m³)	RMSE/Slope	AIC
All species	1 556.7	0.60	94.0	0.060	4 594.8
Category A					
Woody	1 562.0	0.59	229.9	0.147	868.1
Herbaceous	1 472.3	0.81	14.6	0.010	2 646.1
Category B					
Forb	1 740.2	0.79	14.7	0.008	1 547.0
Grass	1 314.0	0.87	13.0	0.010	1 072.1
Shrub	1 562.0	0.59	229.9	0.147	868.1
Category C					
Forb	2 003.8	0.70	11.5	0.006	1 008.0
Subshrub	1 675.1	0.84	19.6	0.012	514.0
Leafy shrub	983.7	0.84	94.3	0.96	374.3
Sclerophyllous shrub	3 831.5	0.93	115.0	0.030	398.9
Long-life grass	1 310.7	0.88	16.7	0.013	613.6
Short-life grass	2 365.2	0.38	6.2	0.003	407.1
Species specific					
Maireana pyramidata	3 696.5	0.98	89.0	0.024	194.0
Atriplex vesicaria	2 360.8	0.97	7.0	0.003	146.0
Sclerolaena ventricosa	3 174.5	0.95	11.5	0.004	128.4
Ptilotus sessilifolius	1 023.1	0.80	4.4	0.004	183.9
Abutilon halophilim	1 659.0	0.85	28.5	0.017	157.5
Astrebla lappaceae & A. pectinata	1 301.2	0.89	20.5	0.016	368.4
Thyridolepis mitchelliana	8 873.0	0.41	5.6	0.001	199.5
Eragrostis setifolia	1 627.7	0.72	8.9	0.005	228.0
Maireana sedifolia	6 553.3	0.84	95.9	0.015	196.3
Sida petrophila	727.5	0.89	3.8	0.005	120.6
Austrostipa scabra	2 134.8	0.82	3.8	0.002	65.8
Sclerolaena eriacantha	2 944.5	0.86	4.3	0.001	154.5
Eremophila gilesii	983.7	0.84	94.3	0.096	374.3
Rhodanthe floribunda	1 410.6	0.75	4.6	0.003	157.7
Calotis lappulacea	805.3	0.53	6.3	0.008	206.7

measurements to generate a *cover·height index;* 2) determine if equations based on data from multiple plant species, covering different growth forms and life histories, were suitable for estimating AGB and address the level of specificity required for species groupings for accurate estimation of AGB; and 3) determine if landscape-scale estimates derived from multisite data were suitable for use at the site level, for six sites in eastern Australian rangelands. We found that the addition of *height* to *cover* (i.e., *cover·height index*) improved allometric model fits in several groups but reduced the fits for others. Generally, model fits were improved with increasing specify of plant groups; however, this was not always the case. With respect to performance of allometric equations to predict AGB in validation plots, we found *cover*-based estimates to be superior to *cover·height index*–based measurements at five of

six sites. In addition, increasing specificity of plant functional groups improved AGB estimates in validation plots when using *cover.*

When comparing allometric equations on the basis of adjusted R^2, 7 of the 12 categories tested were improved (0.2–11.0% improvement) by the addition of height (i.e., using the *cover·height index*), compared with *cover* alone, while the remaining 5 were less accurate (−8.3% to −0.5% change). Using RMSE, we found similar results; estimates that improved when height was added performed in much the same way using both RMSE and R^2 metrics. On the basis of AIC selection criteria, four groups were significantly improved with the *cover·height index,* while only two groups were negatively affected. We conclude that the inclusion of height to *cover*-based estimates of AGB generally yields more accurate

Table 5
Changes in adjusted R^2, root square mean error (RMSE), and Akaike's information criteria (AIC) when using *cover·height index* to predict aboveground biomass (AGB), compared with use of cover data alone.

Category	Type	Adjusted R^2 (% change)	RMSE (% change)	AIC (raw improvement)
All species	All species	3.9	−2.7	21.3[1]
Category A	Woody	3.1	−2.1	2.6
	Herbaceous	−2.2	5.3	−33.4[2]
Category B	Forb	−2.1	4.4	16.0[1]
	Grass	0.2	−0.6	1.6
	Shrub	3.1	−2.1	2.6
Category C	Forb	3.6	−3.9	10.3[1]
	Subshrub	−3.5	10.7	−11.8[2]
	Leafy shrub	11.0	−19.3	13.3[2]
	Sclerophyllous shrub	−0.5	3.4	−2.1
	Long-life grass	0.5	−1.7	2.5
	Short-life grass	−8.3	2.9	−3.6

Note: A positive percentage for adjusted R^2 indicates more variation was explained with the addition of height, while a positive percentage for RMSE indicates less variation was explained in the model.
[1] Denotes where the addition of height significantly impmroved the model estimate.
[2] Denotes where the addition of height significantly worsened the estimate.
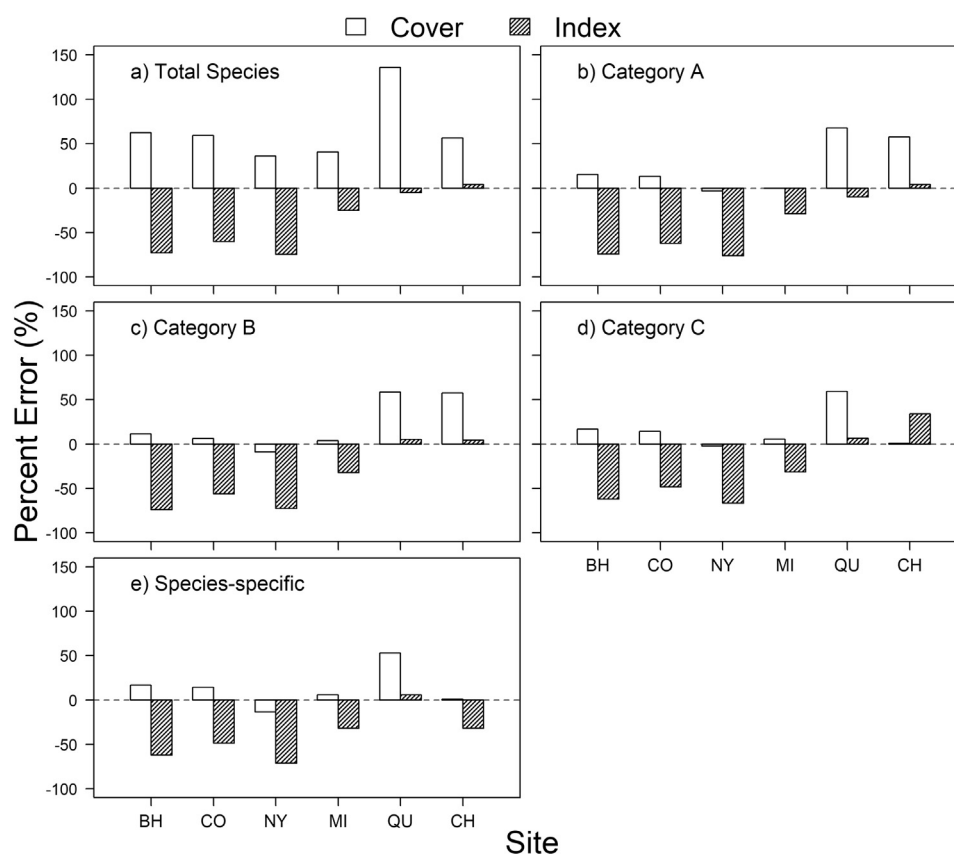
Figure 2. Percent error of standing biomass as predicted by allometric equations using data from total species (panel a), category A (panel b), category B (panel c), category C (panel d), and species-specific data (panel e). Allometric estimates were achieved using *cover* (white bars) and *cover·height index* (dashed bars) as predictors at six sites (BH = Broken Hill, CO = Cobar, NY = Nyngan, MI = Milparinka, QU = Quilpie, CH = Charleville).

estimates, particularly when grouping species at more specific levels. This provides support for our hypothesis that the inclusion of height may be beneficial for cross-site usage. So although efficacy at predicting AGB was typically better using *cover,* the addition of height adds to the robustness of model fits. This may be in part due to the relatively isolated, open nature of the plants selected to build the allometric equations. As height is an important characteristic for competitive interactions in community (Westoby 1998; Falster and Westoby 2005), perhaps its addition in the validation plots causes the mismatch.

The increasing amount of data variance explained (adjusted R^2) and reduced error terms (RMSE) with increasing specificity of plant grouping indicate that species-specific estimates of AGB may be better than multispecies estimates, which was contrary to previous studies (Chojnacky et al. 2013; Roxburgh et al. 2015; Paul et al. 2016), at least in herbaceous (Nafus et al. 2009; Flombaum and Sala 2007) and shrub-dominated plant communities (Buech and Rugg 1989; 1995; Mosseler et al. 2014). Indeed, we found evidence that suggests greater specificity of plant groups will yield improved allometric estimates of AGB when using *cover* at these sites. This remains true if we look at the species-specific data (see Tables 3 and 4), where adjusted R^2 values were greatest, and the ratio of RMSE to the slope was the lowest, for species-specific estimates compared with multispecies estimates. This supports our hypothesis that greater specificity of plant groupings improves model fits for allometric AGB estimates.

The estimates of *cover*-AGB relationships (slopes) for our study were similar to other studies using *cover.* Flombaum and Sala (2007) in the Patagonian steppe found cover-based AGB estimate slopes of 1 225.1 g·m^2 and 596.3 g·m^2 for shrubs and grasses, respectively. Our study indicated slopes ranging from 606.7 g·m^2 to

650.4 g·m^2 for grasses; however, our shrub estimates were quite different. For our leafy woody shrubs (a subgroup of CatC), solely represented by *E. gilesii,* we found a slope of 528.1 while our two sclerophyllous species (CatC) had slopes of 2 106.3 g·m^2. Our estimate based on woody categorization (CatA) was closer to that of Flombaum and Sala (2007) at 863.5 g·m^2, which was derived using both leafy and sclerophyllous species, but they differed markedly from those found by Ónodi et al. (2017), whose slopes for grass *cover*-AGB ranged from 123.7 g·m^2 to 189.9 g·m^2, depending on the year of sampling. It is important to note that estimates presented at the g·m^2 and g·m^3 may be inflated since none of the individuals sampled was actually that size (see Table 2 for range of sizes sampled by species). This likely explains why, at the per-m^3 scale, *forbs* had greater biomass than *shrubs* (see category B in Table 4).

The addition of height, previously considered to add little robustness to predicting AGB in grasses (Andariese 1986; Assaeed 1997; Guevara, Gonnet and Estevez 2002; Nafus et al. 2009), improved our model fits in some cases. There has been an increase in interest in why allometric estimates may not be accurate across years and across sites (Frank and McNaughton 1990; Sala et al. 2000; Shaver et al. 2001; Ónodi et al. 2017). We see the addition of height as a possible mechanistic explanation for changes in the proxy-AGB relationship across temporal and spatial scales, particularly in grasslands where shifts from water to light limitation can occur (Knapp 1984). In other words, periods of high water availability may result in greater aboveground growth (to avoid being shaded), which would not be apparent in the *cover*-AGB relationship. The improvement of allometric fits with *height* in this study (Table 5) occurred for "total species," *forbs* (Cat B and Cat C), and *leafy shrubs* (Cat C); however, the addition of height negatively affected the estimates of AGB in the *herbaceous* group (Cat A).

Interspecific differences among plant organ size (e.g., leaf size) and structure (e.g., specific leaf area) may limit the use of multispecies estimates, which others have considered in herbaceous systems (Frank and McNaughton 1990). Therefore, integration of other, less easily measured proxies for AGB may be necessary to more accurately predict AGB, such as changes in plant tissue density (leaves and stems) that can vary with environmental conditions.

While the addition of *height* improved some allometric model fits, this generally had a negative impact on estimating AGB in the validation plots (except for Quilpie). Overall, the *cover*-based predictions were accurate and improved with specificity, indicating suitable use for future AGB estimates. This is in contrast to the observations of Pottier and Jabot (2017), who found volume as a useful predictor of AGB; however, they did not use cover alone and found that minimum volume was the best estimator of AGB. Our research also contradicts that of Rojo et al. (2017), who found *cover*-based estimates of arid land tussock grasses and shrubs less accurate than those that incorporated *height* and plant diameter. Although these studies assessed cover and additional metrics (e.g., diameter, stem length) to estimate AGB and tested several model fits (e.g., power functions), they did not assess the range of species across broad plant functional types as we did in our study. In the future, a combination of new model fits, a greater number of predictive metrics, and data on new plant functional types will likely be necessary to improve allometric estimates of AGB.

Conclusions

Using 15 species from six field sites in the eastern Australian arid and semiarid rangelands, we conclude that using a *cover·height index* was marginally superior to *cover* alone in generating robust allometric model fits across all sites. While model fit was improved with the addition of *height* to *cover*, we found that *cover* alone was superior at predicting standing AGB in validation plots at five of the six sites. In addition, model fits were improved by grouping data into more specific plant functional groups, despite decreasing the number of samples used to generate the model. Allometric estimates from models using more specific plant groupings improved AGB prediction when using *cover*. Estimates of AGB from *cover·height index* were generally less accurate and would not be recommended for use in the future. While other similar research has emphasized unique equations for allometric purposes or using multiple plant characteristics as proxies for AGB, few have examined how plant functional types may influence nondestructive estimates of AGB. In the future, research should focus on adding more species within existing plant functional type allometric estimates, as well as expanding the number of groups represented to best predict standing AGB in eastern Australian rangelands.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2020.01.009.

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