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Allometric models for aboveground biomass estimation of small trees and shrubs in African savanna ecosystems

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ABSTRACT

Quantification of plant biomass and carbon in ecosystems is critical for establishing climate change mitigation potential. For large trees in various ecosystems, allometric models for estimating biomass have been developed but few biomass equations exist for small trees and shrubby vegetation. Allometric above-ground biomass (AGB) models are needed for small trees and shrubs in order to improve the quantification of biomass, particularly for savanna ecosystems, where small trees and shrubs comprise a significant portion of the biomass. In this study we have developed species-specific and multi-species allometric models for biomass estimation of small tree species and shrubs in the savanna ecosystem of Lake Mburo National Park in South Western Uganda. For our models we selected 27 small tree species (N = 403 individuals) and 12 shrub species (N = 177) common in savanna ecosystems for destructive sampling. We developed species-specific and multi-species allometric AGB models to provide estimates of AGB using specific biometric variables recorded for the small trees (i.e. species, DBH, height and crown area), and shrubs (species, height and crown area). We found that crown area was the best single predictor of species-specific AGB for small trees and for species-specific and multi-species models for shrubs. Species-specific models had the best predictive capacity of AGB compared to multi-species biomass models for small trees and shrubs. Multiple-variable models had the best predictive capacity of AGB in both species-specific and multi-species modeling compared to single-variable models. Based on these findings we conclude that the evaluation of carbon stocks of tropical savanna ecosystems should use multi-variable species-specific models for AGB estimation at the individual level, and multi-species models for AGB at the ecosystem level.

1. Introduction

Quantification of carbon stored in terrestrial ecosystems is an important part of climate change research because these systems sequester carbon and influence the rate of carbon release (Ali and Yan, 2017; Pan et al., 2011; Scurlock and Hall, 1998). Biomass is an important variable in the measurement of carbon pools, and so knowledge about biomass contributes to our understanding of the magnitude and dynamics of carbon stocks. Biomass estimation in terrestrial ecosystems has primarily focused on forests because of their relatively high contribution in regulating carbon. However, tropical savannas are being increasingly recognized as playing a significant role in carbon sequestration (Ali and Yan, 2017). Plants store most of the carbon in the majority of ecosystems so their biomass is a major factor for understanding and modeling carbon storage and dynamics. For example, in tropical forests 56% of carbon storage is in biomass (Pan et al., 2011). Therefore, plant biomass estimation is an important proxy for estimating carbon stocks. This is the rationale for using biomass (or carbon) estimates within the UN's REDD+ initiative (Reducing Emissions from Deforestation and Forest Degradation 'plus' conservation of forests, enhancement of forest carbon stocks and sustainable management of forests; (www.redd.unfccc.int).

Plant biomass can be effectively estimated using 'destructive' sampling methods (Cabrera et al., 2018; Chave et al., 2005) whereby plants are harvested and their Diameter at Breast Height (DBH), total height, wood specific gravity and crown area are subsequently related to the plant's mass (Abich et al., 2021; Chave et al., 2014; Conti et al., 2013). To quantify biomass there is need for allometric modeling approaches.

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For instance, generic allometric models (e.g. the Pan African AGB models; Brown et al. 1997, Chave et al. 2014), and site-specific biomass equations for single and mixed species (Abich et al., 2022; Altanzagas et al., 2019) have been developed for estimating above-ground biomass (AGB) from vegetation measurements such as DBH, height and crown area. These site-specific biomass models are important because size–biomass relationships can show regional differences as plants alter allocation patterns in response to soils, climate and disturbance (Northup et al., 2005). Allometric AGB models may be developed using a single variable (often DBH) or as an additive function of several variables. (e.g. as height, wood density etc.). These additive models that include additional predictors usually improve the accuracy of species biomass predictions (Abich et al., 2021; Ganamé et al., 2021).

One issue for AGB carbon stock measurements is that they are commonly restricted to allometric models for large trees (DBH $\geq$ 5 cm) (Chave et al., 2005; Clough et al., 2018; Henry et al., 2011; Mugasha et al., 2013), whereas models for small trees ($<$ 5 cm DBH) and shrubs that may comprise a large component of some biomes (e.g. tropical savanna) are scarce or unavailable (Ali et al., 2015; Conti et al., 2013; Zeng et al., 2010). Estimating the AGB of small trees and shrubs by applying general biomass allometric models developed for large trees tends to over- or under-estimate the plant biomass (Litton and Boone Kauffman, 2008), with the direction and degree of estimation error related to site-specific factors. Thus, to improve the accuracy of AGB and carbon stock estimation, locally developed AGB models should be used, when available because site-specific allometric models provide more accurate estimates of AGB when compared to Pan Africa allometric AGB models (Aneseyee et al., 2021; Ganamé et al., 2021). The same improvements in accuracy can be expected of species-specific AGB models compared to multi-species models when estimating biomass (Ketterings et al., 2001).

With an increasing global focus on the importance of natural systems to sequester carbon, it is critical to generate AGB models that accurately reflect the plant species and biomes under consideration. In the tropics, multi-species allometric models are often a practical option for estimating AGB because of the coexistence of many different species in these ecosystems. Due to the paucity of allometric models for small trees and shrubs in these tropical systems, studies often ignore their biomass estimation (and hence underestimating the total ecosystem carbon) or apply inappropriate models developed for larger trees. Selecting models for the estimation of AGB is a key problem that we sought to address by comparing different model selection processes. Therefore, we set out to develop and compare several allometric models for the estimation of AGB of small trees and shrubs in a tropical savanna ecosystem in Africa. These equations may provide an important step in carbon accounting studies for payment for REDD+ credits, for REDD+ participating countries such as Uganda.

2. Materials and methods

2.1. Study area

This study was conducted in Lake Mburo National Park (hereafter 'Mburo') and adjacent ranchlands in Kiruhura District, South-Western Uganda. Mburo is approximately 260 km^2 in area, located at 0° 40′ 0″ S and 30° 56′ 0″ E. Adjacent ranchlands are privately owned and managed for livestock production. The climate of the region falls within the Ankole Southern climate zone, situated at an elevation of ~1200 m with mean annual precipitation of ~800 mm and mean annual temperature of 22 °C temperature (Blösch, 2002). The vegetation is of savanna ecosystem classified as grassland, open woodland and dense woodland but currently modified by woody encroachment of *Acacia hockii* (Blösch, 2002; Rannestad et al., 2006). The most abundant woody species are *Acacia hockii, Acacia gerradii, Rhus natalensis, Grewia trichocarpa, Scutia myrtina, Dichrostachys cinerea* and *Maytenus heterophylla* (Blösch, 2002; Moe et al., 2009).

2.2. Species selection

The most common woody species present in the Mburo area were selected (Nyamukuru et al., 2019). Twenty-seven small tree species ($\leq$ 5 cm, DBH) and 12 shrub species were selected. Fourteen to 16 individuals per species were destructively sampled from four paired sites of 1060 m^2 on either side of the border in ranchlands across Mburo (Appendices 1 and 2; Fig. 1). We cut down individual small trees and shrubs to ground level, and divided into stem, branches and leaves for each individual. Shrubs having fruits, were weighted separately for fruits. For very small individuals, we considered stem and branches to be one part (see Nyamukuru et al. 2019 for detailed sampling design). In order to incorporate the different plant size ranges, some individuals outside the sites but within the study area were sampled.

2.3. Biomass measurements

In total, we sampled 403 small tree and 177 shrub individuals. Before the destructive procedure, we recorded the following biometric variables for small trees: the species, DBH (cm), total tree height (m), and their maximum crown diameters and their perpendicular diameters (m) to quantify the crown area. For shrubs we recorded the species, crown area and height (m). The crown area was quantified by measuring the maximum crown diameter and its perpendicular diameter following Conti et al. (2013).

We weighed stems, branches and leaves of each individual small tree and shrub in the field to determine the fresh weight. After weighing, we collected a sub sample of stem wood, branches, leaves and fruits of each individual per species. Each sample was immediately weighed and later oven dried at 80 °C until a constant weight was obtained to determine the dry to fresh weight ratio. The dry weight was obtained for each section as a product of mean dry to fresh ratio and the fresh weight of the respective plant section. Total dry weight was the sum of stem, branches and leaves and fruits for some individuals. The mean dry to fresh weight ratio was computed for stem, branches, leaves and fruits for each sampled individual plant.

2.4. Statistical analysis

Linear regression is an important tool for AGB modeling (Gao et al., 2018). We derived multi-species AGB regression models that related AGB to biometric variables for small trees (Appendices 1 and 2). In addition, species-specific AGB models were derived using log-transformed response and explanatory variables. Log transformed variables in AGB regressions are commonly used (e.g. Altanzagas et al. 2019, Conti et al. 2013, Overman et al. 1994, Packard et al. 2011) because it helps reduce the influence of heteroscedasticity (Baskerville, 1972).

We utilised two different model selection processes in developing the allometric equations for both the multi-species and species-specific models. The first approach being a single explanatory variable AGB equation based on the best fitted univariate model: using either DBH, height or crown area as the explanatory variable related to AGB. The second was a multiple-variables equation that allowed the inclusion of any combination of explanatory variables. For these we selected highest-ranked multi-species and species-specific models based on the Akaike Information Criteria (AIC) to minimize issues associated with overfitting. While acknowledging that other model formulations may also sometimes have substantial support from the data, we present the highest-ranked models based on AIC because these are the most likely models to best explain the relationships between the explanatory variables and AGB (Burnham and Anderson, 2004). For each model we also calculated the predictive mean squared error from model residuals, adjusted coefficient of determination (R^2) and a correction factor of all tested models. We computed the correction factor following (Parresol, 1999) to correct for bias in biomass estimation due to natural log

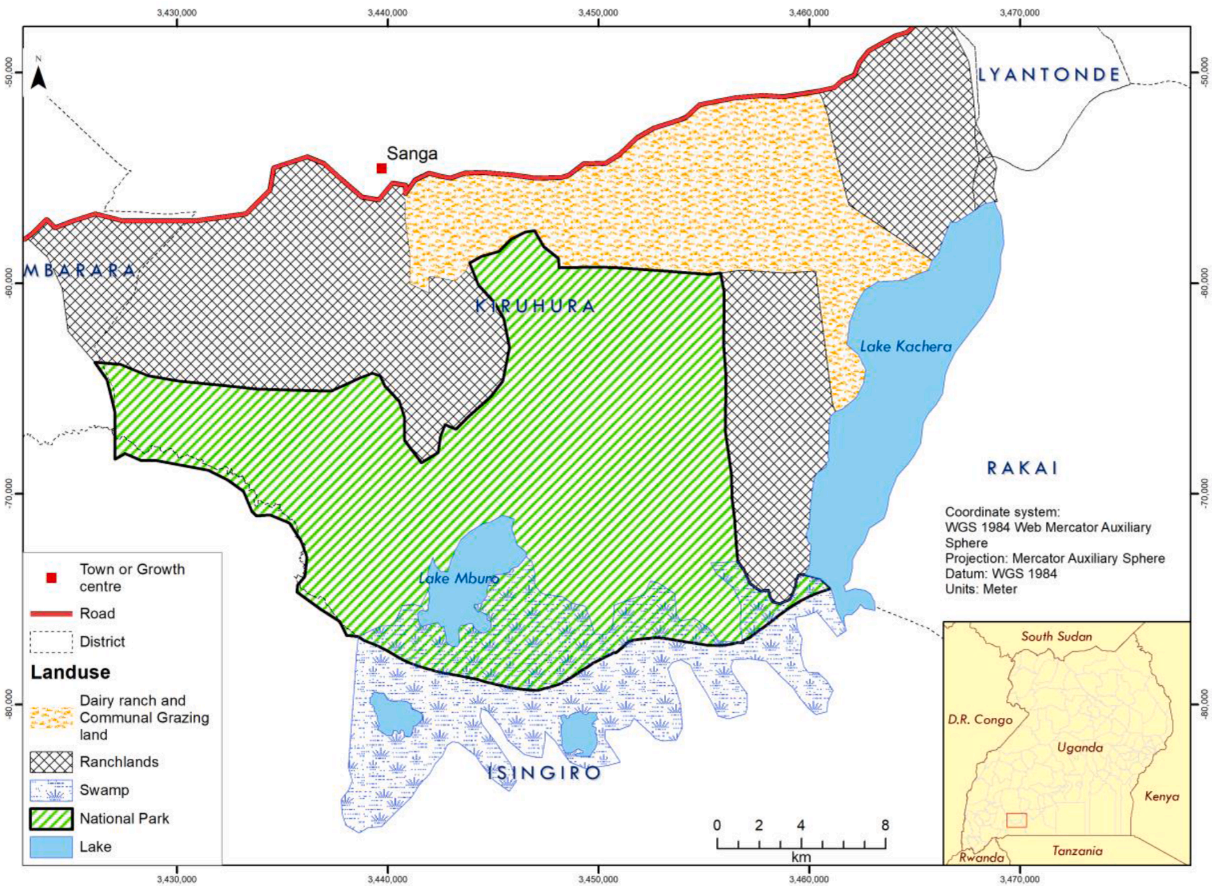

Fig. 1. Location of study sites in Lake Mburo National Park and adjacent ranchlands in Uganda.

transformation. We validated the best AGB models using leave-one-out cross validation methods described by Paul et al. (2018). From this we calculated two validation metrics: (1) the percentage bias, to tests how much the model over or under estimates AGB on average (ideally this lies between −20% and +20%), and (2) we computed the p-values of the residual errors using a t-test to see if the prediction error of the model on the original data significantly differed from the prediction error of the leave-one-out data (where the p-value should ideally be >0.05).

3. Results

Measurements of biometric characteristics varied among the studied species (Table 1). Small trees with the highest DBH (range 0.80–4.90 cm) included *Acacia gerrardii, Pappea capensis* and *Maytenus senegalensis*

Table 1
Summary of biometric variables (CA = crown area; DBH = diameter at breast height; H = plant height) and aboveground biomass (AGB) for small trees and shrubs. These are summarised based on the mean, minimum, maximum and standard deviation (STD) for all individuals sampled (N). The DBH of shrubs was not measured.

Plants	CA (m^2)	DBH (cm)	H (m)	Observed AGB (kg)
Shrubs (n=177)				
Mean	2.68		1.35	0.2
Min	0.13		0.26	0
Max	22.23		3.06	1.64
SD (±)	3.49		0.64	0.27
Small trees (n=403)				
Mean	7.29	2.5	2.21	1.11
Min	0.09	0.5	0.25	0.01
Max	43.33	4.9	5.87	18
SD (±)	7.07	1.05	1.03	1.69

among others. The tallest species in the study area were *Euclea racemose, Olea africana* and *Ziziphus mucronata,* with the average height of these species ranging between 1.01 and 4.76 m. For shrubs, the tallest species (total height) included *Lantana camara, Erythrococca bongensis* and *Rytigynia beniensis* and their average height ranged between 0.90 and 3.06 m. *Dichrostachys cinarea, Acacia gerrardii* and *Ziziphus mucronata* had the largest crown area (35.39 m^2). For shrubs, *Lantana camara, Erythrococca bongensis* and *Ocimum gratissimum* had the highest total AGB and also had the largest crown area (22.23 m^2).

Among the tree species considered, *Rhus natalensis, Euclea racemosa* and *Acacia gerrardii* had the highest total above-ground biomass. The average AGB ranged between 0.01 and 18 kg. For shrubs, *Erythrococca bongensis, Lantana camara* and *Ocimum gratissimum* had the highest total above-ground biomass and their average AGB ranged between 0.02 and 1.64 kg (Table 1).

3.1. Species-specific above-ground biomass regression models

Among the single-variable models developed for small trees, DBH was the best predictor of AGB for seven species (Table 2). The best fit corresponded to *Maytenus senegalensis* ($R^2 = 0.92$) and *Acacia sieberiana* ($R^2 = 0.90$). Height was the best predictor of AGB for ten species with the best fit corresponding to *Rhus natalensis* ($R^2 = 0.93$), *Grewia bicolor* and *Tarenna graveolens* ($R^2 = 0.90$) whereas crown area best predicted AGB for ten species with the best fit corresponding to *Teclea nobilis* ($R^2 = 0.96$) and *Dichrostachys cinarea* ($R^2 = 0.92$). For shrubs, among the single-variable models, crown area was the best predictor variable for AGB for all species except *Rytigynia beniensis* whose best predictor was height (Table 2). The best fit corresponded to *Solanum dasyphyllum* ($R^2 = 0.89$) and *Ocimum gratissimum* ($R^2 = 0.80$). Crown area was the best single variable predictor in our above-ground biomass regression models

Table 2
Species-specific aboveground biomass regression models for shrubs and trees in the savannah ecosystem of Lake Mburo National Park, Uganda. AGB_p = predicted above-ground biomass (kg), Ln = natural logarithm, DBH = diameter at breast height (cm), Height = total plant height (m) and CA = crown area (m^2). Model descriptions include R^2 = coefficient of determination (adjusted for the number of independent variables), PMSE = predictive mean squared error, CF = correction factor, AIC = Akaike information criterion, RTT = residual t-test, and %Bias = Percentage bias. The residual t-test should be $p > 0.05$, and the percentage bias between −20% and +20%. All regressions for small trees were statistically significant at $p < 0.001$, with the exception of *Carissa edulis* and *Grewia similis* where the significance level was $p < 0.05$. Regressions for shrubs were also statistically significant at $p < 0.001$ except for *Achyranthes aspera* whose single variable model was $p < 0.05$. On one occasion where the adjusted R^2 was <0, it is reported as 0.

Species	Model	Fixed parameters	R^2	PMSE	CF	AIC	RTT	%Bias
Small trees								
Acacia gerrardii	Single variables	$\ln(AGB_p) = -2.2214 + 1.0335 \times \ln(CA)$	0.71	0.58	1.40	40.49		
		$\ln(AGB_p) = -3.1881 + 2.9365 \times \ln(DBH)$	0.85	0.31	1.20	31.15	0.98	0.44
		$\ln(AGB_p) = -1.9921 + 2.8232 \times \ln(Height)$	0.82	0.36	1.23	33.38		
	Multiple variables	$\ln(AGB_p) = -2.8654 + 1.7142 \times \ln(DBH) + 1.4659 \times \ln(Height)$	0.92	0.14	1.09	21.59	0.63	−14.17
Acacia hockii	Single variables	$\ln(AGB_p) = -3.0575 + 1.2713 \times \ln(CA)$	0.83	0.15	1.09	20.41	0.50	−14.52
		$\ln(AGB_p) = -2.0339 + 1.7103 \times \ln(DBH)$	0.75	0.22	1.14	26.14		
		$\ln(AGB_p) = -2.8030 + 3.0050 \times \ln(Height)$	0.82	0.16	1.09	20.72		
	Multiple variables	$\ln(AGB_p) = -3.2006 + 0.7129 \times \ln(CA) + 1.6588 \times \ln(Height)$	0.92	0.06	1.04	9.43	0.56	−7.52
Acacia polyacantha	Single variables	$\ln(AGB_p) = -3.9881 + 1.4391 \times \ln(CA)$	0.82	0.13	1.08	18.04	0.50	−23.43
		$\ln(AGB_p) = -2.7767 + 1.9966 \times \ln(DBH)$	0.82	0.14	1.08	18.77		
		$\ln(AGB_p) = -1.8673 + 2.2009 \times \ln(Height)$	0.82	0.14	1.08	18.66		
	Multiple variables	$\ln(AGB_p) = -2.9436 + 0.3879 \times \ln(CA) + 0.8945 \times \ln(DBH) + 0.8975 \times \ln(Height)$	0.92	0.05	1.04	8.25	0.40	−15.22
Acacia sieberiana	Single variables	$\ln(AGB_p) = -3.4055 + 1.4953 \times \ln(CA)$	0.88	0.20	1.12	24.63		
		$\ln(AGB_p) = -2.1510 + 2.3101 \times \ln(DBH)$	0.90	0.16	1.10	20.95		
		$\ln(AGB_p) = -2.6317 + 3.1409 \times \ln(Height)$	0.91	0.15	1.09	19.95	0.33	−21.78
	Multiple variables	$\ln(AGB_p) = -2.4946 + 1.6980 \times \ln(Height) + 1.1725 \times \ln(DBH)$	0.95	0.08	1.05	11.97	0.45	−8.41
Allophylus africanus	Single variables	$\ln(AGB_p) = -2.6665 + 1.1109 \times \ln(CA)$	0.82	0.20	1.12	24.23	0.72	10.41
		$\ln(AGB_p) = -2.3635 + 1.9535 \times \ln(DBH)$	0.67	0.36	1.23	33.33		
		$\ln(AGB_p) = -3.0090 + 2.5972 \times \ln(Height)$	0.64	0.40	1.26	34.64		
	Multiple variables	$\ln(AGB_p) = -3.1581 + 0.6208 \times \ln(CA) + 1.1263 \times \ln(Height) + 0.4901 \times \ln(DBH)$	0.91	0.08	1.06	15.57	0.94	2.01
Boscia salicifolia	Single variables	$\ln(AGB_p) = -2.16553 + 1.07764 \times \ln(CA)$	0.89	0.22	1.13	27.13	1.00	0.12
		$\ln(AGB_p) = -3.3197 + 2.3231 \times \ln(DBH)$	0.84	0.31	1.19	32.52		
		$\ln(AGB_p) = -2.4958 + 3.3348 \times \ln(Height)$	0.83	0.34	1.21	34.14		
	Multiple variables	$\ln(AGB_p) = -2.7574 + 0.4674 \times \ln(CA) + 1.2444 \times \ln(Height) + 0.7515 \times \ln(DBH)$	0.97	0.05	1.03	7.18	0.94	1.16
Carissa edulis	Single variables	$\ln(AGB_p) = -2.1718 + 0.6642 \times \ln(CA)$	0.43	0.26	1.16	28.36		
		$\ln(AGB_p) = -2.2284 + 1.2892 \times \ln(DBH)$	0.33	0.30	1.19	30.71		
		$\ln(AGB_p) = -2.3994 + 2.0873 \times \ln(Height)$	0.47	0.24	1.15	27.28	0.81	−10.27
	Multiple variables	$\ln(AGB_p) = -2.7616 + 1.6232 \times \ln(Height) + 0.8205 \times \ln(DBH)$	0.57	0.18	1.12	24.8	0.93	−3.00
Combretum molle	Single variables	$\ln(AGB_p) = -2.3671 + 1.2101 \times \ln(CA)$	0.71	0.39	1.25	34.55		
		$\ln(AGB_p) = -2.4772 + 1.8731 \times \ln(DBH)$	0.66	0.46	1.30	36.84		
		$\ln(AGB_p) = -2.7829 + 3.0142 \times \ln(Height)$	0.73	0.37	1.24	33.57	0.74	−9.5
	Multiple variables	$\ln(AGB_p) = -2.9597 + 1.5506 \times \ln(Height) + 0.6914 \times \ln(DBH) + 0.4298 \times \ln(CA)$	0.87	0.15	1.11	24.03	0.98	0.65
Commiphora africana	Single variables	$\ln(AGB_p) = -2.7961 + 1.3180 \times \ln(CA)$	0.77	0.30	0.19	30.52		
		$\ln(AGB_p) = -3.7810 + 2.9542 \times \ln(DBH)$	0.87	0.17	1.10	22.17	0.81	−5.09
		$\ln(AGB_p) = -3.4323 + 3.7462 \times \ln(Height)$	0.85	0.20	1.12	24.12		
	Multiple variables	$\ln(AGB_p) = -3.7650 + 1.6906 \times \ln(DBH) + 1.8049 \times \ln(Height)$	0.90	0.12	1.08	18.48	0.62	−11.74
Dichrostachys cinarea	Single variables	$\ln(AGB_p) = -3.6737 + 1.4333 \times \ln(CA)$	0.92	0.17	1.11	22.27	0.72	6.32
		$\ln(AGB_p) = -2.9624 + 2.8348 \times \ln(DBH)$	0.81	0.43	1.28	35.75		
		$\ln(AGB_p) = -2.2417 + 2.6701 \times \ln(Height)$	0.72	0.64	1.28	41.87		
	Multiple variables	$\ln(AGB_p) = -3.4583 + 0.9031 \times \ln(CA) + 0.6856 \times \ln(DBH) + 0.5847 \times \ln(Height)$	0.93	0.13	1.09	22.02	0.67	7.81
Erythrina abyssinica	Single variables	$\ln(AGB_p) = -2.7119 + 1.1027 \times \ln(CA)$	0.69	0.40	1.26	34.82		
		$\ln(AGB_p) = -3.1154 + 1.9523 \times \ln(DBH)$	0.64	0.46	1.30	36.9		
		$\ln(AGB_p) = -3.2398 + 3.1972 \times \ln(Height)$	0.70	0.38	1.25	34.1	0.91	7.06
	Multiple variables	$\ln(AGB_p) = -3.1936 + 1.9365 \times \ln(Height) + 0.6413 \times \ln(CA)$	0.83	0.20	1.14	26.72	0.86	7.51
Euclea racemosa	Single variables	$\ln(AGB_p) = -1.9772 + 1.1887 \times \ln(CA)$	0.71	0.34	1.22	32.47		
		$\ln(AGB_p) = -1.5497 + 2.2146 \times \ln(DBH)$	0.82	0.21	1.13	25.02	0.57	−5.27
		$\ln(AGB_p) = -3.1467 + 2.9422 \times \ln(Height)$	0.68	0.38	1.24	34.03		
	Multiple variables	$\ln(AGB_p) = -2.7036 + 1.5545 \times \ln(DBH) + 1.4318 \times \ln(Height)$	0.91	0.09	1.06	14.89	0.72	−3.53
Flueggea virosa	Single variables	$\ln(AGB_p) = -3.1283 + 1.2319 \times \ln(CA)$	0.76	0.29	1.18	29.83		
		$\ln(AGB_p) = -3.1557 + 2.6229 \times \ln(DBH)$	0.87	0.16	1.10	20.93	0.75	7.83
		$\ln(AGB_p) = -3.4042 + 2.6128 \times \ln(Height)$	0.62	0.46	1.30	36.89		
	Multiple variables	$\ln(AGB_p) = -3.5242 + 2.0644 \times \ln(DBH) + 0.9188 \times \ln(Height)$	0.90	0.11	1.07	17.00	0.98	0.54
Grewia bicolor	Single variables	$\ln(AGB_p) = -3.3778 + 1.5682 \times \ln(CA)$	0.85	0.46	1.31	34.88		
		$\ln(AGB_p) = -3.055 + 2.907 \times \ln(DBH)$	0.74	0.79	1.59	42.45		

(*continued on next page*)

Table 2 (*continued*)

Species	Model	Fixed parameters	R^2	PMSE	CF	AIC	RTT	%Bias
		$\ln(AGB_p) = -2.9581 + 3.2151$ x $\ln(Height)$	0.90	0.30	1.19	28.8	0.49	−23.4
	Multiple variables	$\ln(AGB_p) = -3.1904 + 2.2279$ x $\ln(Height) + 0.5371$ x $\ln(CA)$	0.91	0.25	1.17	28.3	0.80	−3.98
Grewia similis	Single variables	$\ln(AGB_p) = -2.5507 + 0.8702$ x $\ln(CA)$	0.47	0.70	1.50	43.32	0.58	−24.08
		$\ln(AGB_p) = -1.7579 + 1.4255$ x $\ln(DBH)$	0.15	1.14	1.93	50.49		
		$\ln(AGB_p) = -1.5468 + 0.8465$ x $\ln(Height)$	0.12	1.18	1.97	51.02		
	Multiple variables	$\ln(AGB_p) = -2.6234 + 0.7904$ x $\ln(CA) + 0.3119$ x $\ln(Height)$	0.45	0.68	1.52	44.68	0.59	−23.05
Maytenus heterophylla	Single variables	$\ln(AGB_p) = -2.8866 + 1.4040$ x $\ln(CA)$	0.57	0.89	1.68	44.13		
		$\ln(AGB_p) = -3.8390 + 3.5694$ x $\ln(DBH)$	0.82	0.38	1.25	32.08	0.46	−18.52
		$\ln(AGB_p) = -1.3188 + 1.4315$ x $\ln(Height)$	0.42	1.21	2.03	48.40		
	Multiple variables	$\ln(AGB_p) = -3.9777 + 2.8666$ x $\ln(DBH) + 0.4482$ x $\ln(CA)$	0.84	0.31	1.22	31.34	0.42	−16.17
Maytenus senegalensis	Single variables	$\ln(AGB_p) = -2.4288 + 1.3241$ x $\ln(CA)$	0.80	0.40	1.26	34.66		
		$\ln(AGB_p) = -3.1518 + 2.6598$ x $\ln(DBH)$	0.92	0.15	1.09	20.10	0.97	−0.74
		$\ln(AGB_p) = -2.3215 + 2.8429$ x $\ln(Height)$	0.55	0.87	1.65	46.52		
	Multiple variables	$\ln(AGB_p) = -3.2372 + 2.2524$ x $\ln(DBH) + 0.8234$ x $\ln(Height)$	0.95	0.09	1.06	14.84	0.86	3.30
Ochna hackarsii	Single variables	$\ln(AGB_p) = -2.3692 + 1.2549$ x $\ln(CA)$	0.76	0.56	1.39	37.73		
		$\ln(AGB_p) = -2.9321 + 2.6845$ x $\ln(DBH)$	0.74	0.63	1.44	39.15		
		$\ln(AGB_p) = -3.0674 + 2.8307$ x $\ln(Height)$	0.88	0.29	1.19	28.57	0.44	29.91
	Multiple variables	$\ln(AGB_p) = -3.0838 + 1.4891$ x $\ln(Height) + 0.9241$ x $\ln(DBH) + 0.3319$ x $\ln(CA)$	0.91	0.17	1.13	25.01	0.36	33.46
Olea africana	Single variables	$\ln(AGB_p) = -2.2000 + 1.0739$ x $\ln(CA)$	0.77	0.41	1.26	35.07		
		$\ln(AGB_p) = -2.5860 + 2.5921$ x $\ln(DBH)$	0.67	0.59	1.40	40.62		
		$\ln(AGB_p) = -4.0843 + 3.7681$ x $\ln(Height)$	0.86	0.24	1.15	27.38	0.57	−22.47
	Multiple variables	$\ln(AGB_p) = -3.9549 + 2.9604$ x $\ln(Height) + 0.7960$ x $\ln(DBH)$	0.88	0.02	1.13	26.13	0.61	−15.23
Pappea capensis	Single variables	$\ln(AGB_p) = -1.5312 + 1.0185$ x $\ln(CA)$	0.82	0.38	1.24	33.91	0.70	−10.78
		$\ln(AGB_p) = -3.3689 + 3.0500$ x $\ln(DBH)$	0.78	0.45	1.30	36.67		
		$\ln(AGB_p) = -3.1875 + 3.2733$ x $\ln(Height)$	0.73	0.57	1.39	40.17		
	Multiple variables	$\ln(AGB_p) = -2.5404 + 0.6119$ x $\ln(CA) +1.5049$ x $\ln(DBH)$	0.88	0.24	1.16	28.98	0.97	−0.81
Rhus natalensis	Single variables	$\ln(AGB_p) = -2.4975 + 1.4279$ x $\ln(CA)$	0.88	0.44	1.29	36.35		
		$\ln(AGB_p) = -2.8730 + 2.6001$ x $\ln(DBH)$	0.74	0.97	1.75	48.05		
		$\ln(AGB_p) = -2.9342 + 3.1174$ x $\ln(Height)$	0.93	0.28	1.18	29.49	0.67	16.44
	Multiple variables	$\ln(AGB_p) = -2.8735 + 1.9183$ x $\ln(Height) + 0.6406$ x $\ln(CA)$	0.97	0.11	1.07	17.77	0.62	17.42
Scutia myrtina	Single variables	$\ln(AGB_p) = -2.0700 + 0.7934$ x $\ln(CA)$	0.64	0.32	1.20	31.33		
		$\ln(AGB_p) = -1.9793 + 1.4321$ x $\ln(DBH)$	0.44	0.49	1.33	37.94		
		$\ln(AGB_p) = -2.4456 + 2.1073$ x $\ln(Height)$	0.69	0.27	1.17	28.91	0.59	−21.06
	Multiple variables	$\ln(AGB_p) = -2.7884 + 1.3596$ x $\ln(Height) + 0.5951$ x $\ln(DBH) + 0.2980$ x $\ln(CA)$	0.88	0.09	1.06	16.06	1.00	−0.01
Tarenna graveolens	Single variables	$\ln(AGB_p) = -1.1209 + 0.9283$ x $\ln(CA)$	0.55	0.88	1.67	43.95		
		$\ln(AGB_p) = -2.3941 + 2.4634$ x $\ln(DBH)$	0.80	0.39	1.26	32.61		
		$\ln(AGB_p) = -3.3859 + 3.1955$ x $\ln(Height)$	0.90	0.20	1.12	22.91	0.47	−26.47
	Multiple variables	$\ln(AGB_p) = -3.2156 + 2.2653$ x $\ln(Height) + 0.8806$ x $\ln(DBH)$	0.92	0.14	1.09	20.01	0.72	−5.29
Teclea nobilis	Single variables	$\ln(AGB_p) = -2.80297 + 1.40435$ x $\ln(CA)$	0.96	0.12	1.07	17.05	0.91	2.46
		$\ln(AGB_p) = -3.3955 + 3.2678$ x $\ln(DBH)$	0.79	0.68	1.48	42.79		
		$\ln(AGB_p) = -2.6074 + 2.9307$ x $\ln(Height)$	0.90	0.33	1.21	32.02		
	Multiple variables	$\ln(AGB_p) = -2.8091 + 1.0074$ x $\ln(CA) + 0.9291$ x $\ln(Height)$	0.97	0.08	1.05	11.79	0.78	−4.55
Ximenia americana	Single variables	$\ln(AGB_p) = -2.5661 + 1.1361$ x $\ln(CA)$	0.89	0.12	1.07	16.83	0.86	3.80
		$\ln(AGB_p) = -2.7457 + 1.9725$ x $\ln(DBH)$	0.78	0.25	1.16	27.97		
		$\ln(AGB_p) = -2.9345 + 3.5710$ x $\ln(Height)$	0.78	0.25	1.15	27.63		
	Multiple variables	$\ln(AGB_p) = -2.8742 + 0.7754$ x $\ln(CA) + 1.5271$ x $\ln(Height)$	0.95	0.05	1.03	6.47	0.80	3.97
Zanthoxylum chalybeum	Single variables	$\ln(AGB_p) = -2.3141 + 1.2178$ x $\ln(CA)$	0.88	0.20	1.12	25.47	0.77	−4.68
		$\ln(AGB_p) = -2.6759 + 2.5379$ x $\ln(DBH)$	0.87	0.23	1.14	27.65		
		$\ln(AGB_p) = -2.9470 + 3.4416$ x $\ln(Height)$	0.73	0.46	1.30	39.03		
	Multiple variables	$\ln(AGB_p) = -2.7838 + 0.7083$ x $\ln(CA) + 0.8178$ x $\ln(Height) + 0.7873$ x $\ln(DBH)$	0.96	0.06	1.04	10.09	0.85	3.27
Ziziphus mucronata	Single variables	$\ln(AGB_p) = -4.2420 + 1.8207$ x $\ln(CA)$	0.74	0.32	1.20	31.48		
		$\ln(AGB_p) = -2.4011 + 2.5292$ x $\ln(DBH)$	0.87	0.17	1.10	21.84	0.64	−6.47
		$\ln(AGB_p) = -2.254 + 2.422$ x $\ln(Height)$	0.82	0.23	1.14	26.36		
	Multiple variables	$\ln(AGB_p) = -2.5196 + 1.5581$ x $\ln(DBH) + 1.1371$ x $\ln(Height)$	0.92	0.10	1.06	15.32	0.51	−8.84
Shrubs								
Achyranthes aspera	Single variables	$\ln(AGB_p) = -3.2214 + 0.3794$ x $\ln(CA)$	0.20	0.48	1.32	37.56	1.00	0.69
		$\ln(AGB_p) = -3.1741 + 0.6137$ x $\ln(Height)$	0.00	0.62	1.43	41.36		
Asparagus racemosus	Single variables	$\ln(AGB_p) = -3.6477 + 0.8103$ x $\ln(CA)$	0.52	0.14	1.09	19.34	1.00	−1.74
		$\ln(AGB_p) = -3.5880 + 0.6168$ x $\ln(Height)$	0.01	0.30	1.19	30.28		
	Multiple variables	$\ln(AGB_p) = -3.6667 + 0.7835$ x $\ln(CA) + 0.2001$ x $\ln(Height)$	0.49	0.14	1.09	21.07	0.99	−2.11

(continued on next page)

Table 2 (*continued*)

Species	Model	Fixed parameters	R^2	PMSE	CF	AIC	RTT	%Bias
Capparis fascicularis	Single variables	$\ln(AGB_p) = -1.8740 + 0.4942 \times \ln(CA)$	0.55	0.10	1.06	14.68	0.99	0.44
		$\ln(AGB_p) = -2.0576 + 1.1993 \times \ln(Height)$	0.50	0.11	1.07	16.08		
	Multiple variables	$\ln(AGB_p) = -2.1023 + 0.3380 \times \ln(CA) + 0.7569 \times \ln(Height)$	0.69	0.07	1.04	9.72	0.96	1.64
Erythrococca bongensis	Single variables	$\ln(AGB_p) = -1.9424 + 0.7097 \times \ln(CA)$	0.70	0.20	1.12	24.40	0.89	−3.97
		$\ln(AGB_p) = -2.9961 + 2.3460 \times \ln(Height)$	0.31	0.45	1.30	36.71		
	Multiple variables	$\ln(AGB_p) = -3.03777 + 0.61384 \times \ln(CA) + 1.48990 \times \ln(Height)$	0.83	0.10	1.07	16.76	0.91	−2.59
Hoslundia opposita	Single variables	$\ln(AGB_p) = -3.2061 + 0.6346 \times \ln(CA)$	0.68	0.12	1.07	16.23	0.98	−5.16
		$\ln(AGB_p) = -3.1822 + 1.8113 \times \ln(Height)$	0.52	0.18	1.11	21.75		
	Multiple variables	$\ln(AGB_p) = -3.20845 + 0.46816 \times \ln(CA) + 0.76245 \times \ln(Height)$	0.71	0.10	1.07	15.65	0.99	−1.96
Lantana camara	Single variables	$\ln(AGB_p) = -2.5813 + 0.9314 \times \ln(CA)$	0.71	0.19	1.12	23.72	0.68	−12.11
		$\ln(AGB_p) = -2.5383 + 2.6146 \times \ln(Height)$	0.48	0.34	1.22	32.42		
	Multiple variables	$\ln(AGB_p) = -2.58923 + 0.91943 \times \ln(CA) + 0.04786 \times \ln(Height)$	0.68	0.19	1.13	25.72	0.67	−12.7
Ocimum basilicum	Single variables	$\ln(AGB_p) = -3.1941 + 1.3302 \times \ln(CA)$	0.82	0.13	1.07	17.38	1.00	−0.21
		$\ln(AGB_p) = -1.9657 + 3.2390 \times \ln(Height)$	0.35	0.44	1.29	36.42		
	Multiple variables	$\ln(AGB_p) = -2.1732 + 1.1458 \times \ln(CA) + 1.6855 \times \ln(Height)$	0.91	0.06	1.04	7.70	0.99	2.96
Ocimum gratissimum	Single variables	$\ln(AGB_p) = -2.7011 + 0.9951 \times \ln(CA)$	0.80	0.20	1.12	22.92	0.90	6.12
		$\ln(AGB_p) = -2.6050 + 2.3003 \times \ln(Height)$	0.66	0.34	1.22	30.51		
	Multiple variables	$\ln(AGB_p) = -2.7087 + 0.8808 \times \ln(CA) + 0.3243 \times \ln(Height)$	0.79	0.19	1.13	24.7	0.92	4.68
Rytigynia beniensis	Single variables	$\ln(AGB_p) = -1.9490 + 0.4093 \times \ln(CA)$	0.08	0.65	1.45	42.03		
		$\ln(AGB_p) = -2.7919 + 2.7919 \times \ln(Height)$	0.61	0.27	1.17	28.91	0.96	3.08
Sida acuta	Single variables	$\ln(AGB_p) = -3.1996 + 1.4304 \times \ln(CA)$	0.80	0.21	1.13	25.49	0.98	3.72
		$\ln(AGB_p) = -2.9625 + 2.2249 \times \ln(Height)$	0.51	0.52	1.35	38.76		
	Multiple variables	$\ln(AGB_p) = -3.1304 + 1.2260 \times \ln(CA) + 0.5361 \times \ln(Height)$	0.80	0.20	1.13	26.25	0.97	6.89
Solanum dasyphyllum	Single variables	$\ln(AGB_p) = -2.9984 + 1.4336 \times \ln(CA)$	0.89	0.34	1.22	30.45	0.26	−132.6
		$\ln(AGB_p) = -1.7822 + 2.3989 \times \ln(Height)$	0.66	1.07	1.86	46.64	0.69	−45.61
	Multiple variables	$\ln(AGB_p) = -2.6875 + 0.7359 \times \ln(Height) + 1.1442 \times \ln(CA)$	0.91	0.24	1.17	27.95	0.28	−91.21
Solanum incanum	Single variables	$\ln(AGB_p) = -2.5612 + 0.9454 \times \ln(CA)$	0.46	0.39	1.25	34.34	0.90	−15.95
		$\ln(AGB_p) = -2.9135 + 1.4548 \times \ln(Height)$	0.32	0.49	1.33	37.95		
	Multiple variables	$\ln(AGB_p) = -3.0219 + 0.9093 \times \ln(CA) + 1.3774 \times \ln(Height)$	0.80	0.13	1.09	20.32	0.93	6.86

for species-specific regression models of small trees and shrubs. All single-variable models for both small trees and shrubs were significant (Table 2).

Considering multiple-variables models developed for small trees, models with the best predictive capacity were those developed for *Boscia salicifolia* ($R^2 = 0.97$), *Rhus natalensis* ($R^2 = 0.97$), *Teclea nobilis* ($R^2 = 0.97$) and *Zanthoxylum chalybeum* ($R^2 = 0.96$; Table 2). These multiple-variables models had a combination of CA, height and DBH or CA and height. For shrubs, species for which our models had the best predictive capacity combined CA and height and the best fit corresponded to *Solanum dasyphyllum* ($R^2 = 0.91$), *Ocimum basilicum* ($R^2 = 0.91$) and *Erythrococca bongensis* ($R^2 = 0.83$; Table 2).

The validation t-tests for the AGB models were non-significant, showing that the prediction error did not differ between the original data and the cross-validated model predictions. The percentage biases were between −20% and +20% except for *Grewia bicolor, Olea africana, Scutia myrtina, Tarenna graveolens, Ochna hackarsii* and *Grewia similis*. These species had either their single or multiple-variables models above the threshold of the percentage bias, but the residual t-test was within the range (Tables 2 and 3).

3.2. Multi-species above-ground biomass regression models

As observed in species-specific models, crown area was the variable that best predicted AGB for all species. The second best fit for small trees was DBH (Fig. 2a) and height for shrubs (Fig. 3b). A multiple-variable model which included crown area and height provided the best fit for the multiple-species model of shrub AGB ($R^2 = 0.77$, $p < 0.001$) and

Table 3
Multispecies aboveground biomass (AGB) regression models for shrubs in the savannah ecosystem of Lake Mburo National Park, Uganda. AGB_p predicted aboveground biomass (kg), Ln natural logarithm, DBH = diameter at breast height (cm), Height = total plant height (m), CA= crown area (m^2). Model descriptive statistics include R^2 = coefficient of determination, PMSE = predictive mean squared error, CF = correction factor, AIC = Akaike information criterion, RTT = residual t-test, %Bias = Percentage bias. The residual t-test should be p >0.05 and the percentage bias between −20% and +20%.

Model	Fixed parameters	R^2	PMSE	CF	AIC	RTT	%Bias
Shrubs							
Single variables	$\ln(AGB_p) = -2.90239 + 1.07110 \times \ln(CA)$	0.66	0.62	1.37	424.14	0.64	−14.58
	$\ln(AGB_p) = -2.82253 + 2.07100 \times \ln(Height)$	0.62	0.71	1.43	446.99		
Multiple variables	$\ln(AGB_p) = -2.95013 + 0.68960 \times \ln(CA) + 1.16005 \times \ln(Height)$	0.77	0.42	1.24	355.66	0.86	−4.45
Trees							
Single variables	$\ln(AGB_p) = -2.73481 + 2.41305 \times \ln(DBH)$	0.70	0.60	1.35	944.83	0.37	6.03
	$\ln(AGB_p) = -2.50339 + 2.51572 \times \ln(Height)$	0.69	0.62	1.37	960.09		
	$\ln(AGB_p) = -2.40728 + 1.09105 \times \ln(CA)$	0.70	0.60	1.35	944.37	0.93	0.55
	$\ln(AGBp) = -2.98593 + 1.46973 \times \ln(DBH) + 1.48219 \times \ln(Height)$	0.83	0.33	1.18	708.60	0.33	4.87
Multiple variables	$\ln(AGB_p) = -2.99755 + 0.41631 \times \ln(CA) + 1.01003 \times \ln(DBH) + 1.13642 \times \ln(Height)$	0.87	0.25	1.14	600.29	0.28	5.17

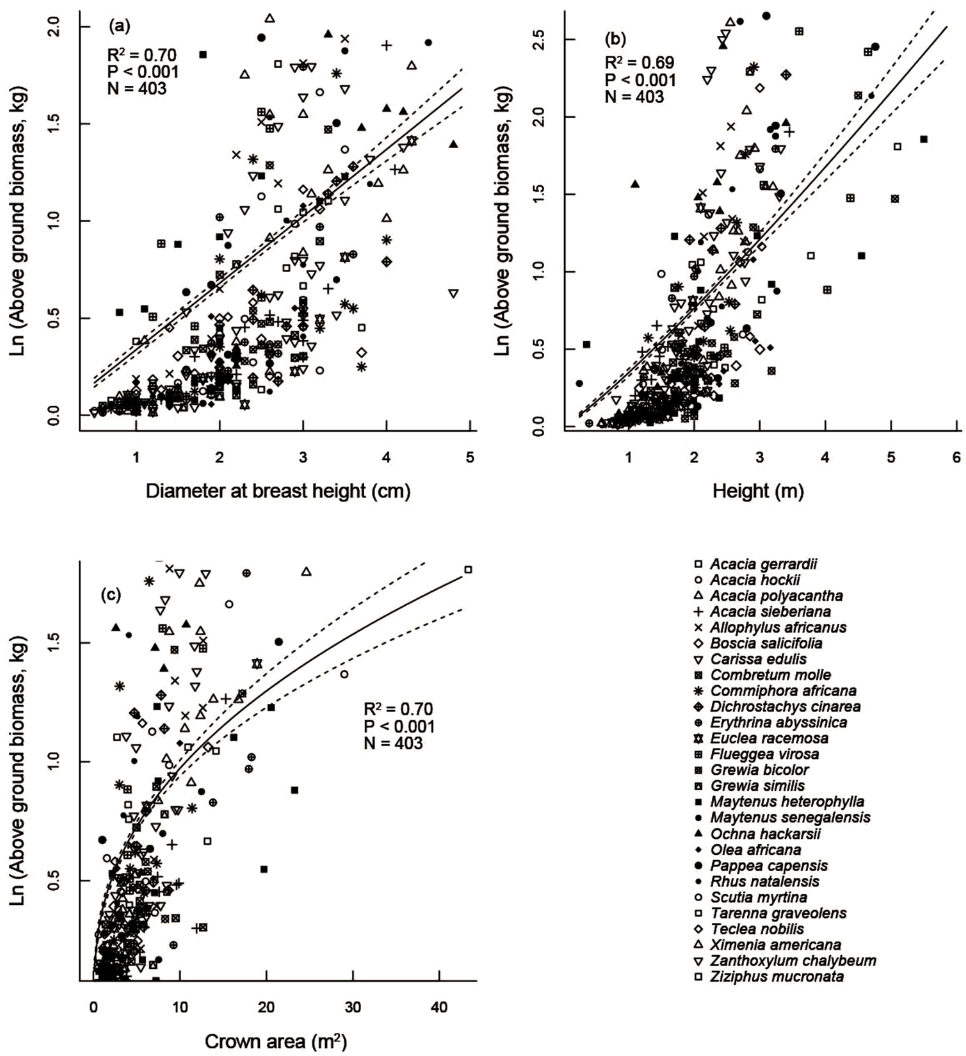

Fig. 2. Relationship of small trees between the above-ground biomass (kg) and diameter at breast height (DBH, cm), height (m) and crown area (m^2) in the savannah ecosystem of Lake Mburo National Park, Uganda. Different symbols represent the different small tree species.

these were the only variables included in the multiple-variables model for shrubs (Table 3; Fig. 4b). All multiple-variables models were significant except for a perennial shrubby herb *Achyranthes aspera* ($R^2 = 0.13$, $p = 0.1726$) in species-specific models (Table 2). For small trees, the best fit of multi-species model includes a model with crown area, DBH and height ($R^2 = 0.87$, $p < 0.001$) (Table 3; Fig. 4a). Table 3 shows the multi-species models for all species of small trees and shrubs.

4. Discussion

Our species-specific models outperformed multi-species biomass models when estimating AGB. This has also been supported in literature (see Abich et al. 2021, 2022, Henry et al. 2011, Pati et al. 2022). Contrary to our results, Fayolle et al. (2013) found that species-specific models were not better than multi-species models in estimating AGB in lowland tropical forests of South-eastern Cameroon. Multi-species models still performed well in estimating AGB and are recommended in situations when species-specific allometric models are lacking for tropical savanna species. We find that multi-species models, such as the ones we have used here, can be useful when estimating AGB for small trees and shrubs in tropical systems. This has also been the case in young reforestations where species-specific and multi-species models provided accurate estimates of AGB (Menéndez-Miguélez et al., 2022).

The performance of multiple-variables models was generally better than single-variable models in both species-specific and multi-species models, although single-variable models still have a good predicative ability. Our results are in agreement with those of Conti et al. (2013) for shrub biomass estimation in the semiarid Chaco forest who found that multiple-variables models performed better than single variable and crown models. However, the authors pointed out that using models with fewer variables are preferred since many variables are laborious and require a lot of attention to validate each variable. Our study found that multiple-variables models that combined three (CA, DBH and height) or two (CA and height) variables had the best predictive capacity of AGB of small trees and shrubs in species-specific models. However, Pati et al. (2022) found that multiple-variables models that combined diameter and height in species-specific models had a better prediction capacity of AGB in tropical dry deciduous forests. Also Feyisa et al. (2018) found that models which combined DBH and height had the best prediction of AGB for selected woody species in East African rangelands.

The fitted species-specific models developed for small trees and shrubs using single-variables show considerable variation among species. For trees, AGB was best predicted using single-variables of height or DBH whereas crown area more accurately predicted AGB of shrubs. This variation likely results from species-specific variations of biometric characteristics of the trees and shrubs in the study area. Despite this general pattern, we highlight that in six tree species (*Acacia hockii, A. polyacantha, A. sieberiana, Carissa edulis, Combretum molle, Erythrina*

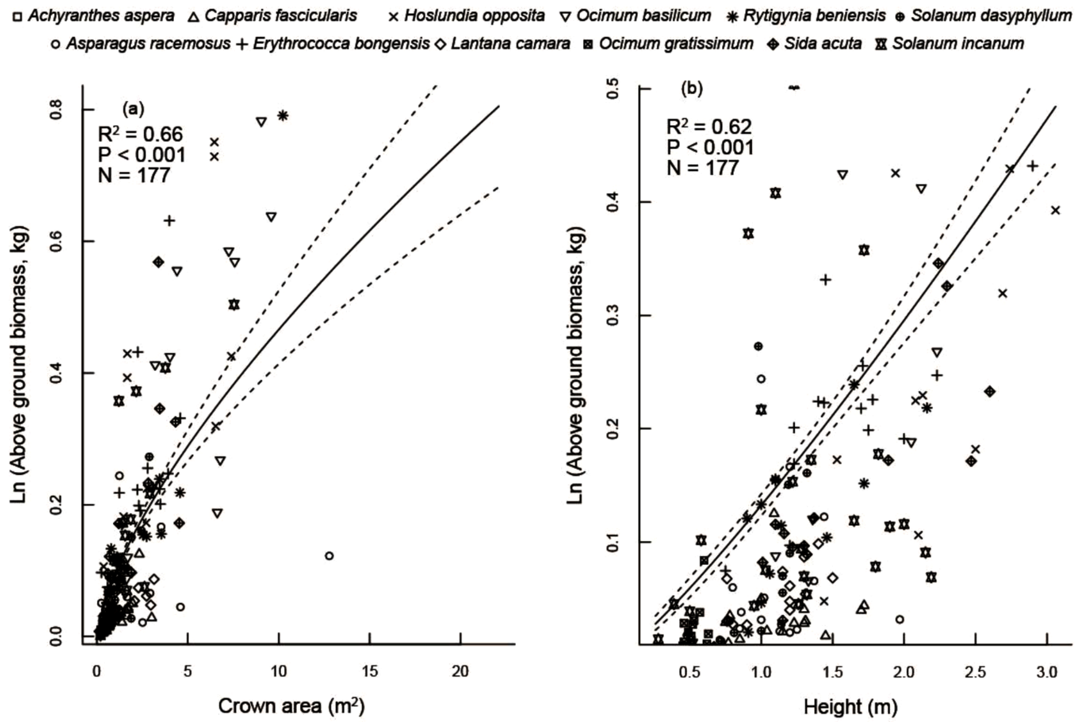

Fig. 3. Relationship of shrubs between the above-ground biomass (kg), height (m) and crown area (m^2) in the savannah ecosystem of Lake Mburo National Park, Uganda. Different symbols represent the different shrub species.

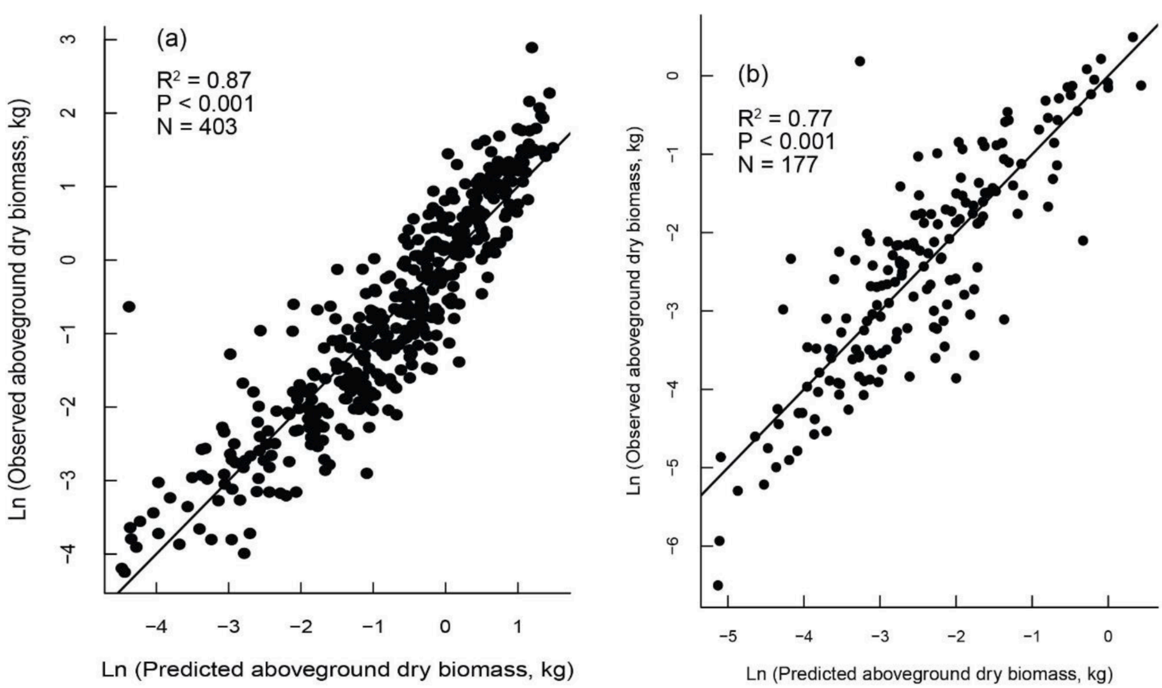

Fig. 4. Multiple-variables model for predicting above-ground biomass for shrubs and trees in the savannah ecosystem of Lake Mburo National Park, Uganda, the models consider all species together, (a) small trees and (b) shrubs. Each dot corresponds to an individual weighted small tree ln(AGBp) = −2.99755 + 0.41631 x ln (CA) + 1.01003 x ln(DBH) + 1.13642 x ln(Height) and shrub ln(AGBp) = −2.95013 + 0.68960 x ln(CA) + 1.16005 x ln(Height).

abyssinia) there was little difference between the model fit of single-variable models using crown area and height (i.e. AIC was often <1 between these models). Thus for some species, there is flexibility in which measure can be used in single-variable modeling for AGB, whereas, for other species, our models indicate a specific variable that best maximizes AGB estimation accuracy (Table 2). Typically, DBH is the best predictor variable for estimating biomass in large trees (Abich et al., 2022), because its predictive capacity is enhanced by the role of the main tree stem in determining AGB (Mukuralinda et al., 2021). Thus, the relative contribution of a tree's main stem to its total volume will determine the predictive importance of DBH versus crown area; here small trees with a high stem-to-crown ratio will be more heavily influenced by DBH in determining the total AGB. It is also worth considering how factors such as DBH and crown area are likely to show regional variation, and how these will tend to influence the site-specificity of AGB measurements (Aneseyee et al., 2021; Dutcă et al., 2018).

The findings of this study show that crown area and total height multiple-variables perform well in multi-species models for estimating AGB for shrubs. This is in agreement with the multiple-variable model reported for Acacia woodland (Aneseyee et al., 2021) and shrubs in semiarid Chaco forests in South America (although this model also included wood specific gravity; Conti et al. 2013), and the recommendation to include architectural plant variables such as height and crown area as additive predictors in models for estimating aboveground biomass for dryland woody species (Bayen et al., 2020). Our AGB models that include these variables appear to provide accurate estimates of biomass, and hence carbon, in the tropical savanna ecosystem at Mburo.

The multi-species model that best predicted AGB in small trees included DBH and height. The finding of DBH and height as the best predictor of AGB for small trees in this study is also supported by Ali et al. (2015). Similarly, DBH and height have been reported as good predictors of AGB for large trees (Chave et al., 2005; Mugasha et al., 2013). A study by Ganamé et al. (2021) that developed allometric models for West African savanna ecosystems reported that species-specific and mixed-species allometric models provided accurate estimates of AGB using DBH and height as predictive variable. In the same study, the authors found that site-specific allometric models for mixed-species and the pantropical allometric model provided similar estimates of AGB.

The fitted multi-species, multiple-variables models for estimating AGB for shrubs showed that crown area and height largely explain the variations in AGB of shrubs (Table 3). Crown area was identified as the best predictor of AGB for shrubs in both multi-species and species-specific models, a finding that has also been reported by other researchers (Conti et al., 2013; Northup et al., 2005; Zeng et al., 2010) who noted a relationship between size and biomass of shrubs. From a practical perspective, crown area for shrubs is relatively quick and easy to measure in the field compared to other biometric variables, adding to its value for the estimation of AGB.

5. Conclusion

This study has developed species-specific and multi-species biomass regression models for providing accurate estimates of AGB of small trees and shrubs of common species in an African savanna. Although accurate estimates of AGB are provided by species-specific AGB models, where these are not available, multi-species biomass models could generate accurate estimations of AGB in similar savanna ecosystems in Uganda and Africa based on the high predictive capacity demonstrated by cross validation. Crown area is the variable that best predicts above-ground biomass in multi-species models. We recommend these AGB models be subsequently used to estimate AGB of small trees and shrubs in savanna ecosystems of Uganda and other parts of Africa until regional-specific AGB models have been developed.

Data statement

All relevant data are within the paper and supplementary materials.

CRediT authorship contribution statement

Antonia Nyamukuru: Conceptualization, Visualization, Investigation, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Cory Whitney:** Writing – review & editing, Visualization. **John R.S. Tabuti:** Conceptualization, Visualization, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Josephine Esaete:** Writing – review & editing, Visualization, Project administration. **Matthew Low:** Visualization, Methodology, Data curation, Formal analysis, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All relevant data are shared in the paper and in the supplementary materials.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2023.100377.

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