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Composition, biomass and structure of mangroves within the Zambezi River Delta

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Abstract We used a stratified random sampling design to inventory the mangrove vegetation within the Zambezi River Delta, Mozambique, to provide a basis for estimating biomass pools. We used canopy height, derived from remote sensing data, to stratify the inventory area, and then applied a spatial decision support system to objectively allocate sample plots among five strata. Height and diameter were measured on overstory trees, saplings and standing dead trees in nested plots, and biomass was calculated using allometric equations. Each of the eight mangrove species occurring in Mozambique exist within the Delta. They are distributed in heterogeneous mixtures within each of the five canopy height classes, not reflecting obvious zonation. Overstory trees averaged approximately 2000 trees ha^{-1}, and average basal area ranged from 14 to 41 m^2 ha^{-1} among height classes. The composition of the saplings tended to mirror the overstory, and the diameter frequency distributions suggest all-aged stands. Above-ground biomass ranged from 111 to 483 Mg ha^{-1} with 95 % confidence interval generally within 15 % of the height class mean. Despite over 3000 trees ha^{-1} in the small-tree component, 92 % of the vegetation biomass is in the overstory live trees. The objective inventory design proved effective in estimating forest biomass within the 30,267 ha mangrove forest.

Keywords Forest inventory · Mangrove biomass · Zambezi River Delta

Introduction

The socioeconomic and ecological importance of mangrove forests are widely recognized (Alongi 2002), and the high carbon density that characterizes these forests has the potential for increasing their value by providing a basis for participation in REDD+ and other carbon trading programs (Alongi 2014). Since the forest vegetation is fundamental to the ecosystem services derived from the wetland, quantifying the structure and distribution of biomass is fundamental for sustainable management and conservation of the resource. Despite the widespread interest in mangroves, there are few inventories of specific land areas. Instead most studies considering the mangrove forest

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approach it from the perspective of zonation or gradients. While synoptic assessments provide information about the area studied, they don't necessarily provide an objective basis for scaling the findings beyond that area. Instead, an inventory based on an objective sampling design is needed to develop unbiased estimates of forest biomass. Recognizing the need to encourage the development of spatially explicit mangrove inventory data, the International Blue Carbon Initiative has recently produced guidelines for assessing mangrove carbon stock (Howard et al. 2014).

Mozambique ranks 2nd in total mangrove area in Africa, containing 3054 km^2 of mangroves (Fatoyinbo and Simard 2013). Approximately 10 % of that mangrove resource is located in the Zambezi River Delta, which extends for 180 km along the coast and approximately 50 km inland. It's the second largest continuous mangrove habitat in Africa (Barbosa et al. 2001). Because of the very remote nature of the Delta, there is little information about the structure and composition of the forest and no studies have quantified the forest structure or compositional characteristics.

Our objective was to quantify the vegetation biomass pools in mangroves within the Zambezi River Delta to provide a baseline for assessing change in vegetation biomass pools in the future. Accordingly, an objective sampling design had to be applied within a specific assessment area. The mangrove forest within the Delta contains inclusions of non-mangrove land cover, those areas were not considered. Similarly, this work did not consider any temporal changes in mangrove areal extent.

Methods

Study area

The Zambezi River Delta (Fig. 1) comprises an area of approximately 12,000 km^2, extending 120 km downstream of the Zambezi and Shire Rivers confluence to the Indian Ocean and 200 km along the Mozambican coastline. The climate of the region is tropical, with a distinct dry winter season from April to October and a wet summer season from October to March (Barbosa et al. 2001; Hoguane 2007). The mean annual precipitation in the coastal portion of the Delta is approximately 1400 mm along the coast, with considerable inter-annual variation (Bento et al. 2007). Mean monthly temperatures range from 27 to 37 °C (GRID-Arendal 2013).

The vegetation of the Zambezi River Delta is a mixture of woodlands, savanna, grasslands, mangroves, and coastal dunes within a mosaic of wetlands (Beilfuss et al. 2001). Mangroves occupy an area of 30,267 ha (Fatoyinbo and Simard 2013), occurring on coastal mud flats (Fig. 1). These mud flats are composed of dark silt and clayey alluvium of marine origin, rich in organic matter (Beilfuss et al. 2001). All mangrove species occurring in Mozambique are present in the Delta: *Sonneratia alba* Smith, *Avicennia marina* (Forsskk.) Vierh., *Rhizophora mucronata* Lam., *Ceriops tagal* (Per.) C.B. Robinson, *Bruguiera gymnorrhiza* (L.) Lam., *Lumnitzera racemosa* Wild., *Heritiera littoralis* Alton, and *Xylocarpus granatum* Koenig. Within the Delta, mangrove associate species tend to occur in elevated areas with less tidal inundation (Vilankulos and Marquez 2000) and include *Guettarda speciosa* L., *Hibiscus tiliaceous* L., and the large fern *Achrostichum aureum* L. (Barbosa et al. 2001; Beilfuss et al. 2001). Thickets of *Barringtonia racemosa* (L.) Spreng., also occur along the furthest upstream reaches of tidal influence within the Delta (Beilfuss et al. 2001).

Inventory design

The inventory area was the entire 30,267 ha of mangrove forest, distributed along the north and south banks of the Zambezi River. We used a stratified random sampling design, using forest canopy height as the strata. Using Ice, Cloud, and land Elevation Satellite/Geoscience Laser Altimeter System (ICE Sat/GLAS) and the Shuttle Radar Topography Mission (SRTM) data, Fatoyinbo and Simard (2013) estimated canopy height for African mangroves (data for Africa is available at: http://www-radar.jpl.nasa.gov/coastal/). Five canopy height classes were distinguished within the Zambezi River Delta: 2–6.9 m (HC1), 7–9.9 m (HC 2), 10–12.9 m (HC 3), 13–17.9 m (HC 4), and 18–29 m (HC 5). These height classes were based on the distribution of canopy height among mangrove pixels (90 × 90 m).

A total of 52 randomly-located plots, 0.52 ha in area, were identified for sampling. A spatial decision support system (SDSS) (Densham 1991) was used to identify plot locations, providing randomization of

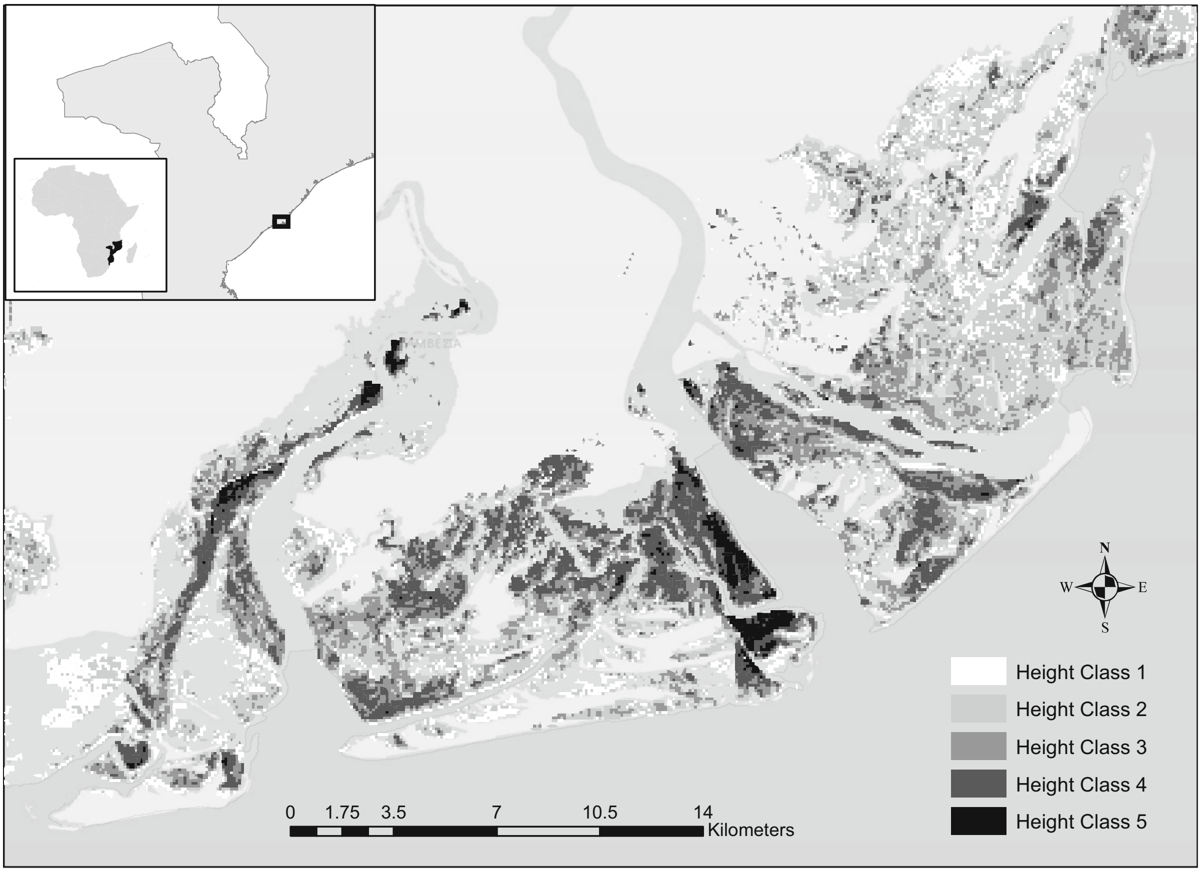

Fig. 1 Distribution of forest canopy height classes within mangroves on the Zambezi River Delta, Mozambique

plot selection and the ability to consider various logistical constraints, as well as ensuring that each plot was located within uniform areas of the strata; defined as minimum of four contiguous pixels (90 × 90 m) in a given height class. Plot locations were identified using algorithms to ensure proper distribution of sampling amongst the height classes. In the event the selected plot proved inaccessible, a randomly selected alternate was used.

The field work was conducted over two field seasons in 2012 and 2013. Our sampling approach used five subplots nested within the 0.52 ha square plot. The purpose of the subplots was to accommodate inherent spatial variation within the plot that was represented in the mangrove stands. The subplot layout consisted of a 7 m radius circle for sampling live trees with a diameter at breast height (DBH) greater than 5 cm and all standing dead trees, containing a nested 2 m radius circle for sampling trees with a DBH smaller than 5 cm.

Tree characteristics

DBH, total height, and species were recorded for overstory trees and saplings in each subplot. Overstory trees, defined by DBH > 5 cm, were measured within the 7 m radius circular subplots. Saplings, defined as all tree with a DBH < 5 cm, were measured in the 2 m radius nested circular subplot. Diameters were measured to the nearest 0.1 cm using a diameter tape. If the tree was dead, a decay class of 1, 2, or 3, as defined by Kauffman and Donato (2012), was recorded in addition to the DBH. Diameter measurements were adjusted to accommodate mangrove morphology as necessary; measurements were taken just above buttresses or the highest prop root. Height was measured

to the nearest 0.5 m for every tree using a hypsometer (Haglof Vertex III, Haglof Inc, Sweden).

Biomass

Above- (B_{AG}, kg) and below-ground (B_{BG}, kg) biomass pools were determined for each live tree, both overstory and understory, using general equations (Komiyama et al. 2005, 2008):

$$B_{AG} = 0.251\, p\, D^{2.46} \quad (1)$$

$$B_{BG} = 0.199\, p^{0.899}\, D^{2.22}$$

where: p represents wood density (g cm^{-3}) and D represents DBH (cm). General equations were selected since local or regional species-specific allometric equations have not been developed. Species-specific p values were estimated as the mid-value of the published density range for each species (World Agroforestry Center 2013). For any tree encountered where the species was unknown, we used the average p among all species present, 0.86 g cm^{-3}.

Above- and below-ground biomass estimates for standing dead trees were conditional on decay class. For the above-ground biomass for decay classes 1 and 2, the same allometric equation used for live trees was applied to each dead tree, using a density of 0.69 g cm^{-3}, as species and wood density were not recorded for dead trees, and it has been considered a reasonable estimate of large solid downed wood (Kauffman and Donato 2012). These estimates were adjusted for the loss of leaves and branches by subtracting 2.5 and 15 % of the biomass for classes 1 and 2, respectively (Kauffman and Donato 2012). The above-ground biomass for class 3 standing dead trees was determined by applying the formula of the volume of a cone. Once volume was determined, the value was multiplied by wood density (0.69 g cm^{-3}) to determine biomass.

Below-ground biomass for all classes of standing dead trees was determined using the same equation used for the live trees, with the standard density value of 0.69 g cm^{-3}. Consideration was made for the swift loss of fine roots once a tree dies. We corrected our estimates by subtracting 46 %, a conservative estimate within the ranges of fine root biomass reported by other studies (Komiyama et al. 1987, 2000). Biomass estimates were converted to carbon mass by using concentration factors of 0.50 and 0.39 for above-ground and below-ground estimates, respectively (Kauffman and Donato 2012).

Statistical analyses

The sampling design consisted of a stratified random sample with five height class strata. Within each stratum a random sample of plots was selected. Sample means, along with variances and 95 % confidence intervals, were computed for each stratum using PROC SURVEYMEANS (SAS Institute 2011) with plots defined as clusters of subplots and where the finite population correction was ignored because the sampling fraction was very low. Differences between height class and species means were performed with individual Satterthwaite two-sample t tests (PROC TTEST) which allows for unequal variances for the two samples. All two-sample t tests were performed at the 0.05 Type I error rate, and are provided in the electronic supplement. Overall species estimates combined over the 5 height class strata used weights based upon strata area for per hectare estimates of basal area, tree density, above-ground biomass, and below-ground biomass. For overall species estimates of DBH and height, weights consisted of the product of strata area and strata density.

Results

Stand characteristics

The stocking of the mangrove forest within the Zambezi River Delta is dominated by overstory trees (Table 1). Stocking was remarkably consistent among height classes averaging 2036 trees ha^{-1}, and ranging from 1848 to 2235 trees ha^{-1}. The diameter distribution of the overstory trees exhibited an inverse J-shape curve which is characteristic of uneven-aged stands (Fig. 2b). The stocking in smaller diameter classes was less pronounced in HC 4 and 5, reflecting the overall larger stature of the stands. Overstory tree diameter weighted mean was 10.4 cm and height was 9.4 m, with relatively little variation among height classes (Table 1). Both overstory tree diameter and height were greater in HC4 and 5 than HC1 and 2. Above-ground tree biomass ranged from 110.7 to 482.6 Mg ha^{-1} among the five height classes. The average above-ground biomass content was

Table 1 Mean (SE) diameter, height basal area, stocking, and above- and below-ground biomass for saplings (<5 cm DBH), trees (>5 cm DBH), and standing dead trees for each height class

Height class	Diameter (cm)	Height (m)	Basal area (m^2 ha^{-1})	Stocking (trees ha^{-1})	AGB (Mg ha^{-1})	BGB (Mg ha^{-1})
Saplings (DBH < 5 cm)						
1	2.4 (0.1)a	3.2 (0.6)abc	3.3 (1.6)a	6000 (3030)a	15.3 (7.4)a	9.3 (4.5)a
2	3.0 (0.1)b	4.1 (0.3)a	2.7 (0.8)a	3492 (866)a	14.9 (4.6)a	8.7 (2.6)a
3	3.0 (0.2)b	3.9 (0.4)a	4.0 (2.0)a	4914 (2268)a	22.1 (11.3)a	12.9 (6.6)a
4	2.9 (0.2)ab	3.1 (0.1)b	1.4 (0.5)a	1808 (722)a	7.5 (2.6)a	4.4 (1.5)a
5	2.3 (0.4)ab	2.2 (0.1)c	1.2 (0.6)a	2347 (1564)a	6.0 (2.8)a	3.6 (1.7)a
Overstory trees (DBH > 5 cm)						
1	8.8 (0.5)a	7.0 (0.4)a	13.7 (2.8)a	1853 (305)a	110.7 (23.6)a	48.6 (9.8)a
2	9.7 (0.5)a	7.9 (0.6)a	20.3 (2.8)ab	2199 (200)a	193.3 (32.9)ab	81.4 (12.8)ab
3	10.3 (1.1)ab	10.4 (0.6)b	24.5 (3.1)bc	2235 (333)a	254.7 (40.3)bc	103.5 (15.1)bc
4	12.8 (0.6)bc	12.1 (0.7)b	33.6 (3.2)cd	2045 (135)a	366.7 (41.2)cd	144.3 (14.2)cd
5	14.4 (1.0)c	12.9 (1.0)b	40.8 (4.7)d	1848 (186)a	482.6 (72.5)d	178.7 (24.2)d
Dead standing trees						
1	8.8 (0.9)a	4.7 (0.2)a	1.9 (1.3)a	255 (132)a	10.6 (7.5)a	3.2 (2.2)a
2	9.1 (0.5)a	5.7 (0.3)b	1.3 (0.4)a	158 (34)a	7.2 (2.0)a	2.2 (0.6)a
3	10.2 (0.4)a	6.8 (0.3)c	2.0 (0.4)a	205 (43)a	13.2 (2.7)a	3.6 (0.7)a
4	11.1 (1.0)a	7.2 (0.4)c	2.5 (0.6)a	206 (46)a	18.8 (6.0)a	4.5 (1.2)a
5	10.6 (1.6)a	7.4 (0.3)c	2.2 (0.9)a	162 (54)a	21.9 (9.9)a	4.4 (2.0)a

Within a column, means followed by the same letter are not significantly different at $p = 0.05$, based on Satterthwaite *t* tests

significantly different among height classes, except for HC1–HC2, and HC1–HC3 (Table 1). The overstory trees comprised 91 % of the above-ground tree biomass. Below-ground biomass was approximately 39 % of the above-ground biomass, and it exhibited the same relationship among height classes as the above-ground component. The biomass estimates reflect the combined influence of diameter and tree stocking, hence the parallel response among the components.

Saplings and standing dead trees comprise approximately 14 % of the total basal area, with the balance in the overstory trees. The sapling component has a high stocking density, averaging 3712 trees ha^{-1}, with an average basal area of 2.5 m^2 ha^{-1}. The frequency distribution of saplings exhibited an increase to 3 cm diameter and then a slight decline (Fig. 2a). The saplings averaged 3.3 m in height, with small but statistically significant variation among height classes (Table 1). However, despite the wide range in stocking among the height classes, the estimates of small-tree above- and below-ground biomass weren't different, reflecting variation among plots. The average above- and below-ground biomass of the small-tree strata was 13.1 and 7.8 Mg ha^{-1}, respectively; the below-ground estimate was 59 % of the above-ground biomass.

Standing dead tree density varied from 158 to 255 trees ha^{-1}, comprising between 1.9 and 2.5 m^2 of basal area within the stands (Table 1). The average diameter of the dead trees was 9.9 cm, and the mean didn't vary significantly among height classes (Table 1). The diameter distribution followed the same pattern of the live trees (Fig. 2c), with the highest proportion of dead trees in the 7–9 cm diameter class. The average height of dead trees was 6.4 m; however, this measure reflects crowns in varying stages of decay. Above- and below-ground biomass averaged 14.3 and 3.6 Mg ha^{-1}, respectively; the difference between height classes weren't statistically different.

The average forest biomass was 432 Mg ha^{-1} with above-ground biomass representing 72 % of the total. The standing live trees accounted for 91 % of the biomass, with the balance distributed among the saplings (5 %) and standing dead trees (4 %). The standard error for the biomass estimates was generally less than 15 % of the mean.

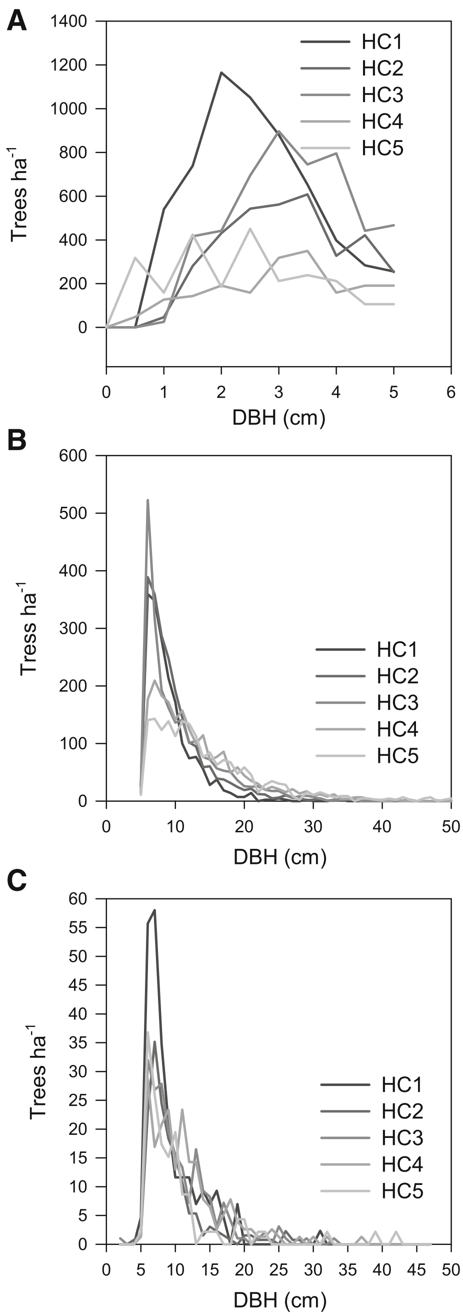

Fig. 2 Diameter frequency distribution within height classes for **a** saplings, **b** live trees, and **c** standing dead trees

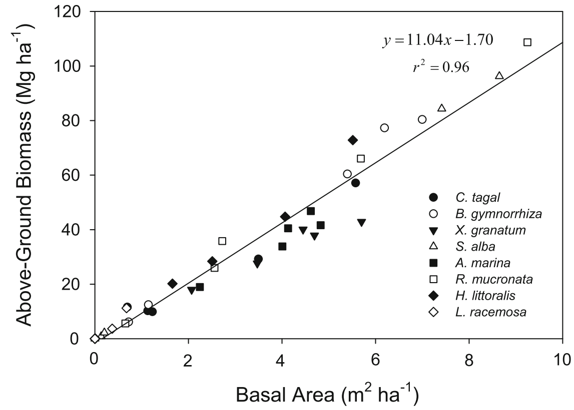

Fig. 3 Relationship of above-ground live tree biomass to species basal area within mangroves on the Zambezi River Delta

Stand composition

All of the mangrove species (8) reported to occur in Mozambique (Beentje and Bandeira 2007) were measured in the Zambezi River Delta, and occurred in varying combinations among the height classes (Table 2); each height class had at least 7 mangrove species, and HC5 had all eight. The mixed nature of the stands is underscored in that 75 % of the basal area was distributed across three or more species in each height classes except HC1 (Table 2). *S. alba* and *B. gymnorrhiza* were the predominant species in the HC4 and 5 stands, collectively comprising 42 and 36 % of the stand basal area, respectively. *R. mucronata* was also prevalent in HC4 (27 %), but comprised only 7 % of the HC5 stands. *X. granatum* and *A. marina* comprise 77 % of the HC1 overstory, and 43 and 32 % respectively of HC2 and 3. *L. racemosa* was relatively rare, occurring in 3 height classes as a minor component of the stands (<2 % of total basal area). Tree density also reflects the mixed nature of the stands (Table 2). Each height class had at least 3 species exceeding 250 stems ha^{-1}. The distribution of tree density for each species among height classes varied considerably; for example, *S. alba* was relatively rare in HC1-3, and dominant in HC4-5, while *A. marina* is well represented in each height class. The average tree diameter was 11.8 cm, varying considerably among species and height classes (Table 2). While mean diameter tended to increase with height class, for *H. littoralis* there wasn't any difference. The largest mean diameter occurred in HC5 (14.3 cm), and there weren't any statistically significant differences among the 8 mangrove species. *B. gymnorrhiza* and *S. alba* had the largest mean diameter in HC3 and 4 respectively. Mean tree height varied among height classes for each species except for *H. littoralis*, but differences among species within a height class were few (Table 2). The overall average tree height was

Table 2 Mean (SE) diameter, height, basal area, stocking, and above- and below-ground biomass by species for trees (>5 cm DBH) within height classes

Height class	*C. tagal*	*B. gymnorrhiza*	*X. granatum*	*S. alba*	*A. marina*	*R. mucronata*	*H. littoralis*	*L. racemosa*	Unknown
Diameter (cm)									
1	7.2 (0.1)	8.0 (0.5)	10.1 (0.7)	6.4 (0.1)	8.9 (0.9)	7.7 (0.2)	–	6.3 (0.0)	9.5 (1.8)
2	7.6 (0.11)	10.8 (2.2)	11.5 (0.8)	14.9 (0.0)	11.1 (1.0)	9.2 (0.8)	11.1 (0.2)	–	11.1 (2.8)
3	7.8 (1.1)	16.0 (1.8)	11.4 (0.6)	–	11.1 (1.0)	11.2 (1.3)	13.2 (0.7)	11.7 (0.2)	9.3 (0.9)
4	9.0 (0.3)	15.9 (1.1)	13.8 (1.2)	22.5 (1.3)	10.3 (0.2)	12.0 (0.9)	10.9 (0.6)	–	14.0 (1.8)
5	15.8 (8.1)	16.2 (2.1)	12.6 (1.5)	15.9 (1.9)	14.8 (1.3)	14.4 (2.7)	11.6 (1.3)	15.1 (0.0)	–
Height (m)									
1	6.8 (0.5)	6.2 (0.4)	7.6 (1.1)	6.4 (0.00)	7.1 (0.5)	6.1 (1.3)	–	5.1 (0.0)	5.2 (0.7)
2	6.4 (0.6)	8.2 (1.1)	8.7 (0.9)	–	7.2 (0.9)	7.3 (1.4)	9.5 (0.1)		6.7 (2.0)
3	9.2 (1.4)	12.1 (0.7)	9.3 (0.5)	–	13.0 (0.1)	10.3 (0.3)	11.8 (1.4)	9.7 (0.2)	11.3 (1.2)
4	10.2 (0.7)	12.8 (1.1)	11.0 (1.0)	18.7 (0.0)	10.6 (0.0)	11.1 (0.2)	10.9 (0.4)	–	10.5 (1.0)
5	11.0 (3.3)	14.3 (0.5)	11.0 (1.1)	15.1 (1.8)	12.6 (0.9)	14.3 (2.2)	10.5 (0.9)	11.9 (0.0)	–
Basal area (m^2)									
1	1.2 (1.0)	0.7 (0.6)	5.7 (3.2)	0.1 (0.1)	4.8 (1.9)	0.7 (0.57)	–	0.01 (0.01)	0.4 (0.3)
2	3.5 (0.9)	1.1 (0.6)	4.7 (1.3)	0.2 (0.2)	4.1 (1.2)	2.6 (1.2)	4.1 (3.2)	–	0.03 (0.02)
3	5.6 (1.8)	5.4 (2.3)	3.5 (1.6)	–	2.2 (1.5)	5.7 (3.3)	1.7 (1.1)	0.4 (0.4)	0.08 (0.05)
4	1.1 (0.6)	7.0 (3.2)	2.1 (0.7)	7.4 (5.4)	4.0 (2.6)	9.2 (4.0)	2.5 (1.5)	–	0.3 (0.2)
5	0.7 (0.5)	6.2 (3.1)	4.5 (2.2)	16.0 (8.0)	4.6 (3.3)	2.7 (2.3)	5.5 (3.0)	0.7 (0.7)	–
Stocking (trees ha^{-1})									
1	285 (224)	116 (91)	601 (337)	39 (36)	631 (200)	132 (115)	–	2 (2)	46 (31)
2	724 (184	85 (46)	371 (90)	8 (8)	326 (70)	334 (119)	348 (274)	–	3 (1)
3	930 (411)	219 (86)	278 (132)	–	208 (126)	464 (230)	96 (65)	29 (28)	11 (8)
4	165 (86)	274 (131)	114 (39)	166 (115)	418 (288)	679 (253)	214 (138)	–	14 (8)
5	19 (12)	219 (118)	275 (158)	591 (268)	229 (185)	132 (73)	366 (232)	17 (18)	–
Above-ground Biomass (Mg ha^{-1})									
1	9.9 (7.8)	6.2 (5.7)	42.9 (24.1)	0.8 (0.8)	41.6 (19.2)	5.6 (4.6)	–	0.1 (0.1)	3.7 (3.1)
2	29.2 (7.2)	12.5 (7.2)	37.9 (11.5)	2.2 (2.2)	40.5 (13.5)	26.0 (12.8)	44.8 (35.7)	–	0.3 (0.2)
3	57.1 (21.4)	60.4 (26.6)	27.7 (12.5)	–	19.0 (12.5)	66.1 (39.6)	20.2 (13.6)	3.7 (3.5)	0.7 (0.4)
4	10.2 (5.1)	80.4 (37.6)	18.0 (6.4)	84.3 (62.3)	33.9 (21.4)	108.7 (47.6)	28.4 (16.5)	–	2.8 (1.8)
5	11.6 (9.0)	77.3 (39.3)	40.1 (19.8)	186.9 (91.7)	46.8 (32.5)	35.8 (31.3)	72.8 (40.1)	11.2 (11.8)	–
Below-ground biomass (Mg ha^{-1})									
1	4.8 (3.8)	2.7 (2.4)	18.6 (10.5)	0.4 (0.4)	17.8 (7.6)	2.7 (2.2)	–	0.02 (0.00)	1.6 (1.3)
2	13.8 (3.4)	4.8 (2.6)	15.9 (4.6)	0.8 (0.8)	16.2 (4.9)	11.3 (5.4)	18.4 (14.7)	–	0.1 (0.1)
3	24.0 (8.3)	23.1 (10.0)	11.7 (5.3)	–	8.3 (5.4)	26.8 (15.8)	7.9 (5.3)	1.5 (1.4)	0.3 (0.2)
4	4.6 (2.3)	30.3 (14.1)	7.3 (2.5)	31.0 (22.7)	14.7 (9.5)	43.9 (19.0)	11.5 (6.7)	–	1.1 (0.7)
5	3.8 (2.7)	27.7 (13.9)	15.8 (7.7)	68.7 (35.1)	18.5 (13.0)	13.6 (11.6)	27.0 (14.5)	3.5 (3.7)	–

Table 3 Mean (SE) diameter, height, basal area, stocking, and above- and below-ground biomass by species for saplings (<5 cm DBH) within height classes

Height class	*C. tagal*	*B. gymnorrhiza*	*X. granatum*	*S. alba*	*A. marina*	*R. mucronata*	*H. littoralis*	*L. racemosa*
Diameter (cm)								
1	2.6 (0.1)	2.2 (0.0)	2.1 (0.1)	3.3 (0.0)	2.5 (0.1)	2.4 (0.0)	–	2.8 (0.0)
2	3.2 (0.2)	2.8 (0.2)	2.6 (0.1)	–	2.3 (0.1)	2.8 (0.5)	2.8 (0.3)	–
3	3.1 (0.3)	3.3 (0.5)	2.6 (0.1)	–	2.8 (0.0)	3.4 (0.2)	2.7 (0.1)	–
4	2.9 (0.1)	4.1 (0.3)	1.8 (0.2)	2.0 (0.0)	2.4 (0.4)	2.7 (0.0)	3.6 (0.3)	–
5	0.7 (0.0)	2.1 (0.1)	–	3.0 (0.0)	–	–	3.2 (0.1)	–
Height (m)								
1	4.5 (0.4)	2.3 (0.0)	2.7 (0.2)	2.4 (0.0)	2.8 (0.2)	3.4 (0.0)	–	3.4 (0.0)
2	4.6 (0.3)	3.0 (0.4)	3.9 (0.4)	–	2.4 (0.4)	3.4 (0.9)	3.0 (0.2)	–
3	4.1 (0.3)	3.3 (0.7)	2.9 (0.2)	–	2.5 (0.3)	4.9 (0.2)	2.3 (0.2)	–
4	2.9 (0.1)	3.5 (0.7)	2.5 (0.1)	1.5 (0.0)	3.5 (0.6)	3.4 (0.1)	3.1 (0.4)	–
5	1.2 (0.0)	2.2 (0.1)	–	2.0 (0.0)	–	–	2.4 (0.1)	–
Basal area (m^2)								
1	1.1 (0.9)	0.4 (0.4)	0.6 (0.3)	0.1 (0.1)	1.0 (0.6)	0.1 (0.1)	–	0.1 (0.1)
2	1.8 (0.7)	0.1 (0.0)	0.2 (0.1)	–	0.1 (0.0)	0.3 (0.2)	0.3 (0.3)	–
3	3.1 (2.0)	0.1 (0.1)	0.2 (0.1)	–	0.03 (0.02)	0.5 (0.4)	0.1 (0.1)	–
4	0.5 (0.5)	0.2 (0.1)	0.1 (0.0)	0.01 (0.01)	0.2 (0.2)	0.1 (0.1)	0.4 (0.3)	–
5	0.01 (0.01)	0.7 (0.6)	–	0.02 (0.02)	–	–	0.5 (0.3)	–
Stocking (trees ha^{-1})								
1	1714 (1323)	800 (764)	1400 (810)	114 (113)	1743 (1277)	143 (136)	–	86 (85)
2	2033 (759)	94 (68)	395 (198)	–	66 (34)	414 (221)	489 (404)	–
3	3797 (2158)	89 (54)	343 (182)	–	51 (39)	508 (382)	127 (94)	–
4	720 (669)	112 (79)	128 (93)	32 (31)	320 (278)	176 (124)	320 (237)	–
5	187 (182)	1573 (1442)	–	27 (26)	–	–	560 (376)	–
Above-ground biomass (Mg ha^{-1})								
1	5.5 (4.6)	2.1 (2.1)	2.1 (1.1)	0.5 (0.5)	4.5 (2.8)	0.3 (0.3)	–	0.3 (0.3)
2	10.0 (4.2)	0.3 (0.2)	0.9 (0.5)	–	0.3 (0.1)	1.7 (0.9)	1.8 (1.3)	–
3	17.3 (11.1)	0.4 (0.3)	0.8 (0.4)	–	0.1 (0.1)	3.0 (2.1)	0.4 (0.3)	–
4	2.8 (2.4)	0.8 (0.6)	0.2 (0.1)	0.1 (0.1)	0.9 (0.7)	0.6 (0.4)	2.2 (1.5)	–
5	0.03 (0.03)	3.0 (2.4)	–	0.1 (0.1)	–	–	2.9 (2.0)	–
Below-ground Biomass (Mg ha^{-1})								
1	3.3 (2.8)	1.3 (1.2)	1.3 (0.8)	0.3 (0.3)	2.7 (1.7)	0.2 (0.2)	–	0.2 (0.2)
2	5.8 (2.7)	0.2 (0.1)	0.5 (0.3)	–	0.2 (0.1)	1.0 (0.5)	1.1 (1.0)	–
3	10.1 (6.4)	0.3 (0.2)	0.5 (0.3)	–	0.1 (0.1)	1.7 (1.2)	0.3 (0.2)	–
4	1.7 (1.5)	0.5 (0.4)	0.1 (0.1)	0.04 (0.03)	0.5 (0.4)	0.4 (0.3)	1.2 (0.9)	–
5	0.02 (0.02)	1.8 (1.5)	–	0.1 (0.1)	–	–	1.7 (1.1)	–

10.2 m, with *C. tagal* having the smallest mean (8.7 m) and *S. alba* the largest (12.9 m). Above-ground biomass for each species corresponded to the total basal area (Fig. 3), demonstrating that basal area can serve as a useful surrogate for biomass.

The sapling component of the stands within height classes was also mixed, averaging six species. In general, the sapling species corresponded with those in the overstory, but their relative composition varied. Each of the mangrove species exhibited a higher proportion of

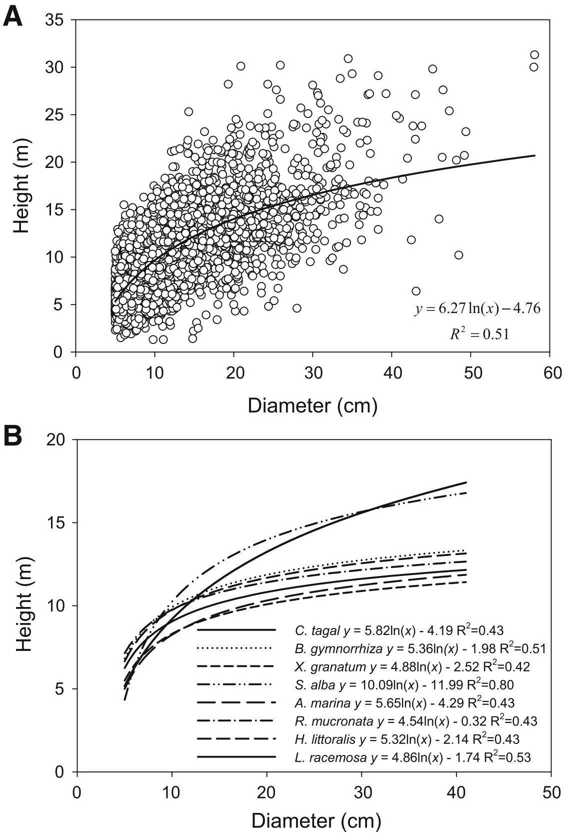

Fig. 4 Relationship of total height to diameter for **a** all live trees (>5 cm DBH) occurring the Zambezi River Delta, and **b** functions derived for each mangrove species

total basal area in the small-tree strata than in the overstory in at least one height class except *R. mucronata*; the most notable was *C. tagal*. The proportional basal area of several species in the sapling strata was lower relative to their occurrence in the overstory, notable are *S. alba* in HC4 and 5, *A. marina* in HC2 and 3, and *B. gymnorrhiza* in HC3. *X. granatum* and *A. marina* had relatively high stocking levels among all height classes, and *C. tagal* was similar except in HC5. In contrast to its prevalence in overstory of HC4 and 5, *S. alba* had relatively low sapling stocking rates (13–14 trees ha^{-1}). Above-ground biomass was generally below 5 Mg ha^{-1} for any given species, reflecting the relatively low stocking and small diameters (Table 3).

The functional relationship between tree diameter and height was effectively described by a log function (Fig. 4a), although there was considerable variability throughout the measured range of tree diameter. Partitioning the response by species indicated similar response among all species except *C. tagal* and *S. alba*, which averaged 2–4 m greater than the other species of the same diameter throughout the Delta (Fig. 4b). *A. marina* and *X. granatum* exhibited the lowest mean height for a given diameter, while *B. gymnorrhiza, R. mucronata,* and *H. littoralis* tended to be slightly taller. Only the correlation coefficient for *S. alba* showed a large improvement in the species-level diameter-height regression function as compared to the function for all mangrove trees (Fig. 4).

In general, the distribution of standing dead trees among species corresponded with the same species as the live tree strata, except HC1. In HC1, *A. marina* comprised 83 % of the standing dead tree basal area, while individuals of *B. gymnorrhiza*, *X. granatum* and *L. racemosa* were absent despite occurring in the overstory. HC5 lacked standing dead trees of *C. tagal* and *L. racemosa* despite occurring in the overstory, but the stocking of those species was quite low in that height class (Table 4).

Discussion

Forest inventory

Forest inventories require an objective sampling design to provide an unbiased assessment of forest components within the assessment area; random, systematic and stratified-random are common sampling designs (Cochran 1977). We chose to utilize a stratified random sampling design in the Zambezi River Delta because it can improve the precision and efficiency of the inventory if there's a basis for the stratification. Since canopy height and stand density are functionally related to stand biomass, the canopy height dataset developed from GLAS/SRTM data by Fatoyinbo and Simard (2013) provided an effective basis for stratifying the mangrove forest within the Delta into classes that were sensitive to differences in stand structure. The application of the stratified sampling design based on spatially-explicit data facilitated the incorporation of a decision support system to ensure that operational constraints did not compromise the objective allocation of sample plots within strata. Jones et al. (2014) also used a stratified sampling design, using land cover and canopy condition classes as the strata, to estimate mangrove biomass

Table 4 Mean (SE) diameter, height, basal area, stocking, and above- and below-ground biomass by species for standing dead trees height classes

Height class	*C. tagal*	*B. gymnorrhiza*	*X. granatum*	*S. alba*	*A. marina*	*R. mucronata*	*H. littoralis*	*L. racemosa*	Unknown
Diameter (cm)									
1	6.7 (0.0)	–	7.0 (0.5)	–	9.1 (1.0)	–	–	–	8.7 (1.3)
2	7.4 (0.5)	8.9 (1.9)	8.3 (0.3)	–	9.6 (0.7)	7.7 (0.4)	14.1 (1.6)	–	9.9 (1.2)
3	8.9 (0.6)	8.7 (2.7)	11.0 (1.0)	5.0 (0.0)	10.2 (1.0)	11.2 (0.8)	15.2 (0.0)	12.1 (0.0)	11.8 (2.3)
4	9.1 (0.5)	14.6 (1.5)	15.5 (2.5)	16.3 (0.0)	9.1 (0.5)	8.9 (1.0)	12.6 (1.0)	–	9.4 (0.7)
5	–	21.4 (9.2)	7.4 (0.1)	6.6 (0.0)	11.6 (1.1)	8.1 (0.0)	10.7 (2.7)	–	8.4 (1.2)
Height (m)									
1	5.3 (0.0)	–	6.1 (1.1)	–	4.4 (0.1)	–	–	–	5.2 (0.3)
2	5.3 (0.2)	5.7 (0.2)	5.5 (0.2)	–	5.6 (0.0)	4.9 (0.7)	6.5 (0.7)	–	6.4 (0.8)
3	6.5 (0.3)	10.6 (2.5)	6.8 (2.5)	–	7.1 (0.0)	6.7 (0.3)	6.2 (0.0)	7.6 (0.0)	5.9 (0.3)
4	6.3 (0.5)	7.3 (0.6)	7.3 (0.6)	8.6 (0.0)	5.9 (0.0)	6.5 (0.4)	8.5 (0.6)	–	6.8 (0.2)
5	–	11.8 (2.6)	5.7 (2.6)	6.4 (0.0)	8.7 (0.0)	2.4 (0.0)	6.7 (1.2)	–	6.9 (0.6)
Basal area (m^2)									
1	0.1 (0.0)	–	0.1 (0.1)	–	1.5 (1.2)	–	–	–	0.2 (0.1)
2	0.1 (0.0)	0.1 (0.0)	0.2 (0.1)	–	0.4 (0.2)	0.1 (0.0)	0.2 (0.2)	–	0.2 (0.1)
3	0.5 (0.2)	0.04 (0.04)	0.5 (0.2)	0.002 (0.002)	0.5 (0.3)	0.2 (0.1)	0.02 (0.02)	0.1 (0.1)	0.2 (0.1)
4	0.2 (0.1)	0.5 (0.2)	0.2 (0.1)	0.3 (0.3)	0.4 (0.3)	0.1 (0.1)	0.5 (0.5)	–	0.2 (0.1)
5	–	0.9 (0.9)	0.1 (0.1)	0.1 (0.1)	0.4 (0.3)	0.01 (0.01)	0.5 (0.3)	–	0.2 (0.1)
Stocking (trees ha^{-1})									
1	12 (11)	–	16 (11)	–	197 (134)	–	–	–	30 (17)
2	27 (7)	8 (4)	31 (10)	–	49 (19)	10 (6)	10 (7)	–	23 (14)
3	69 (18)	5 (4)	45 (22)	1 (1)	47 (32)	12 (6)	1 (1)	9 (9)	14 (8)
4	26 (17)	21 (13)	10 (5)	14 (14)	53 (44)	18 (10)	36 (32)	–	27 (16)
5	–	17 (9)	30 (21)	13 (14)	30 (27)	2 (2)	37 (29)	–	32 (22)
Above-ground biomass (Mg ha^{-1})									
1	0.2 (0.2)	–	0.4 (0.4)	–	8.5 (7.1)	–	–	–	1.4 (0.8)
2	0.6 (0.2)	0.4 (0.2)	0.9 (0.3)	–	2.5 (1.2)	0.2 (0.1)	1.5 (1.1)	–	1.1 (0.8)
3	3.1 (0.9)	0.3 (0.3)	3.2 (1.3)	0.01 (0.01)	3.7 (2.1)	1.2 (0.6)	0.1 (0.1)	0.9 (0.9)	0.8 (0.6)
4	1.2 (0.9)	3.5 (1.9)	1.6 (1.0)	3.1 (3.1)	2.3 (1.7)	0.8 (0.5)	4.9 (4.9)	–	1.5 (0.9)
5	–	10.2 (9.5)	0.7 (0.5)	0.3 (0.3)	2.7 (2.4)	0.02 (0.02)	6.2 (6.2)	–	1.8 (1.0)
Below-ground biomass (Mg ha^{-1})									
1	0.1 (0.1)	–	0.1 (0.1)	–	2.6 (2.2)	–	–	–	0.4 (0.2)
2	0.2 (0.1)	0.1 (0.1)	0.3 (0.1)	–	0.7 (0.3)	0.1 (0.0)	0.4 (0.3)	–	0.4 (0.2)
3	0.9 (0.3)	0.1 (0.1)	0.9 (0.3)	0.003 (0.003)	0.8 (0.5)	0.3 (0.2)	0.03 (0.03)	0.2 (0.2)	0.4 (0.3)
4	0.3 (0.2)	0.9 (0.5)	0.4 (0.3)	0.6 (0.6)	0.6 (0.5)	0.2 (0.1)	1.0 (1.0)	–	0.4 (0.4)
5	–	2.0 (1.9)	0.2 (0.2)	0.1 (0.1)	0.7 (0.5)	0.02 (0.02)	1.0 (0.7)	–	0.4 (0.2)

and carbon stocks within two Bays in northwestern Madagascar. Also within the Indian Ocean basin, Rahman et al. (2014) used a grid approach to inventory the forest conditions in mangroves within the Bangladesh Sundarbans. Inventories implemented with objective sampling designs provide the basis for estimating population attributes with confidence intervals. In contrast, subjectively selected sample plots do not provide unbiased population estimates, and it's not possible to quantify the variability and obtain confidence intervals. Many published estimates of mangrove

biomass stocks are from ad hoc studies, designed for objectives other than inventorying a specified area, and achieve estimates that inform the study but are not necessarily appropriate for quantifying a population (Fromard et al. 1998; Kauffman et al. 2014; Ross et al. 2001; Wang et al. 2013). Accordingly, within the context of REDD+ or other forest inventory purposes, the application of an objective sampling design is required to assess the accuracy of the estimates. In the mangroves within the Zambezi River Delta, our above-ground biomass ranged from 110.7 Mg ha^{-1} in HC1 to 482.6 Mg ha^{-1} in HC5, which is well within the range reported from recent reviews that vary from less than 50 to over 600 Mg ha^{-1} (Alongi 2012).

Forest structure

Mangroves are commonly considered to be even-aged forests, principally developing following a disturbance or colonization of mud flats (Saenger 2002). While we don't have stand age data for the mangroves within the Zambezi River Delta, the physical attributes of the stand reflect an uneven-aged forest. The diameter distribution of both the tree and sapling strata is characteristic of an uneven-aged forest. The small-tree strata reflected strong recruitment in all height classes, demonstrating that most of the mangroves have a strong capacity to regenerate under closed canopies and stands of varying density. Sherman et al. (2000) measured recruitment into gaps in an intertidal mangrove forest in the Dominican Republic, and found that gap size didn't affect regeneration patterns, concluding that gap dynamics weren't a driving factor in the species distribution of mangroves. The ability of the mangrove species to regenerate under widely varying conditions and correspondence of species in the tree and small-tree strata are also indicative of uneven aged forests. Accordingly, the persistent mangroves within the Delta have developed into a more complex forest than is typified during the early stages of mud flat colonization or response to disturbance regimes.

The mean tree height varied from 7 to 13 m across the mangrove stands within the Delta, which is within the range reported for the region. The mean tree height of *R. mucronata*, *H. littoralis*, and *B. gymnorrhiza* were well below the upper limit of 25, 21, and 30 m respectively, as reported by Beentje and Bandeira (2007). Conversely, the mean values for *C. tagal* and *L. racemosa* were greater than the 6 and 9 m respectively, reported by the same authors. Since Beentje and Bandeira (2007) reported on range within East Africa, it's not unexpected that the any specific site would be well within the range. However, documenting mean heights greater than the current reported range suggest that the Zambezi Delta provides new insights regarding the characteristics of *C. tagal* and *L. racemosa* within the region. The range in mean tree height for *A. marina*, *S. alba*, and *X. granatum* corresponded with those reported by Beentje and Bandeira (2007).

The range in mangrove above-ground biomass density (110.7–482.6 Mg ha^{-1}) within the Zambezi Delta is within the range typically reported for mangroves (Fromard et al. 1998), but significantly larger than the 58 Mg ha^{-1} reported in Sofala Bay mangroves in Mozambique (Sitoe et al. 2014). Sitoe et al. (2014) used site-specific allometric equations to estimate stand biomass but did not provide other stand structure data to facilitate comparisons of the mangrove forests. While site-specific allometric equations are preferred as opposed to the general mangrove equations (Komiyama et al. 2008), the two-eight fold difference seems excessively large. A simplistic comparison of the Sitoe et al. (2014) allometric function suggests an error, as their function indicates a tree of 30 cm DBH will contain 22 kg of biomass as contrasted with over 800 kg using the general mangrove equation (Komiyama et al. 2008); the 22 kg estimate for above-ground biomass is unreasonable.

Stand composition

The mangrove forest within the Zambezi River didn't exhibit the large scale zonation that has become a stereotype of mangroves (Kathiresan and Bingham 2001). However, many studies reporting on mangrove zonation aren't necessarily representative of the landscape; instead they're based on a subjective selection of plots, located typically along a few transects, with no provision for knowing whether the sample population is representative of the forest stand or landscape. So while the work may provide information about the study site, there's no objective basis for generalization. Ellison et al. (2000) tested the zonation paradigm based on an objective design in the Bangladesh Sundarbans, and concluded zonation did

not occur, instead that zonation was likely an artifact of studies designed to describe them. Correspondingly, Smith (1992) concluded that despite the numerous descriptive studies describing zonation, there haven't been rigorously designed studies which prove the functional mechanisms that might cause zonation. The forest within each of the height classes in the Zambezi Delta were heterogeneous mixtures of mangrove species occurring in East Africa. Accordingly, while using height class as a basis for stratification reflects physical structure by definition, our data demonstrate that the species distribution was not the driver of the observed structural attributes. Instead the eight mangrove species suggest a wide ecological amplitude given their occurrence throughout the Delta. Detailed zonation studies can provide insights into the species—site relationships (Sherman et al. 2003, Smith 1992). For example in the East Africa region, studying a single transect 280 m long in Gazi Bay, Matthijs et al. (1999) attributed variations in species composition to gradients of soil pH, salinity, and sulfide. However, whether the observed gradient is representative of the landscape is indeterminate.

There are indications that site conditions may influence the expression of species within the Zambezi Delta. For example, *S. alba* is predominant in HC4 and 5, while a minor component of the HC1 and 2 (Table 2). Others are relatively uniformly distributed across the entire forest (e.g. *A. marina*, *X. granatum*, and *C. tagal*). From this perspective, the structural attributes of the stands within height classes may reflect variation in site conditions. Unfortunately, we did not collect site attribute data during the inventory; hence we couldn't analyze the species distribution relative to site conditions. The spatial arrangement of height classes shows little evidence of organization, except for HC5, which tended to occur along active channels that likely convey large quantities of freshwater, a factor known to significantly affect the structural development of mangroves (Pool et al. 1977). The long lenticular band of HC5 in the central delta is adjacent to a major channel connecting the estuary; while the large area of HC5 along the main channel of the Zambezi River could be also be expected to have lower salinity due to the freshwater flow.

Variations in site conditions are implied to drive species zonation. Instead, the data from the Zambezi River Delta suggests that distribution of species is robust across the entire wetland complex, and that site conditions may affect the expression of species within the stand. Inventories of mangrove forests would benefit from the collection of site attribute data, including soil pore water salinity, pH, distance to nearest channel, channel salinity, inundation cycle and depth. In this way, as advances are made with respect to linking site conditions to site productivity, there should be a basis for further interpretations of the inventory data.

Conclusion

A stratified random sampling design using forest canopy height was effective for inventorying the forest structure and composition of the mangroves within the Zambezi River Delta. Accordingly, the continental-scale canopy height database could provide a common foundation for mangrove assessments. The merit of using an objective sampling design is that an unbiased estimate of the resource can be determined with quantified uncertainties. Our selection of five canopy height classes was based on the distribution of the data and a subjective assessment of the number of strata that could be effectively managed. While the classes don't have intrinsic meaning, they functioned to effectively categorize areas and to discriminate between areas with varying amounts of biomass density (Mg ha^{-1}). This inventory approach to assessing the forest composition and structure of the Zambezi River Delta mangroves showed that the eight mangrove species are distributed throughout the Delta, occurring in heterogeneous mixtures in each of the five height classes. The expression or development of species within height classes suggests an influence of site factors; unfortunately, we did not collect associative data that may further support that line of interpretation. Subsequent mangrove inventories in the region may benefit if site descriptors were obtained while measuring the vegetation components. Live trees greater than 5 cm in diameter represented over 90 % of the total biomass, and the relationship between stand basal area and above-ground biomass was strong. Accordingly, stand basal area may serve as an effective metric for characterizing stands, if complete measures of height and diameter aren't feasible to obtain. Presently, tree height is of marginal use for estimating biomass because the majority of the

published allometric equations for mangroves only employ tree diameter. However, height information can be useful in distinguishing structural relationships that may reflect inherent differences in productivity or sensitivities to site conditions.

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