

Above ground woody community attributes, biomass and carbon stocks along a rainfall gradient in the savannas of the central lowveld, South Africa

C.M.Shackleton, R.J. Scholes

Abstract

Enumeration of carbon stocks at benchmark sites is a necessary activity in assessing the potential carbon sequestration and possible generation of credits through restoration of intensively impacted sites. However, there is a lack of empirical studies throughout much of the savannas of sub-Saharan Africa, including South Africa. We report an estimation of species specific and site biomass and carbon stocks, and general vegetation structural attributes from three protected areas along a rainfall gradient in the central lowveld, South Africa. Estimates of biomass and carbon stocks were effected through destructive sampling to establish locally derived allometric equations. There was a gradient of increasing woody density, height of the canopy, number of species, density of regenerative stems and a greater proportion of stems in small size classes from the arid locality to the mesic locality, with the semi-arid locality being intermediate. The proportion of spinescent species decreased with increasing rainfall. The mesic locality was significantly more woody than either the arid or semi-arid sites, having double the biomass, four times the density and 40% higher basal area. Above ground carbon pools were also higher; carbon stocks were approximately 9 t/ha for the arid and semi-arid sites and 18 t/ha for the mesic site.

1. Introduction

Savannas are one of the world's major terrestrial ecosystems, comprising between 10% and 15% of the world's land surface, depending upon definition (Scholes and Hall, 1996). Distributed across nearly all the continents, they occur in broad bands between the equatorial forests and mid-latitude deserts. Approximately 50% of the African continent, and one third of South Africa are savannas. They are home to over 30% of the world's population (Solbrig et al., 1991), and consequently experience marked impacts from human activities. Of particular concern are deforestation and land use change activities which reduce or eliminate the biomass of trees and shrubs. This not only alters local nutrient, water and carbon cycles, thereby affecting local livelihood options and agricultural productivity, but also adds to global CO₂ emissions (Miles and Kapos, 2008). However, in many regions intensive land use is not permanent, leading to a mosaic of land use types with varying levels of woody biomass ([Giannecchini et al., 2007] and [Eaton and Lawrence, 2009]) and hence carbon sequestration potential. Consequently, carbon accounting for specific geographic regions needs to be able to accommodate such dynamic changes, benchmarked against relatively un-impacted sites.

The international concern with and modelling of carbon emissions and sequestration requires adequate coverage of locally quantified carbon stocks. However, several authors have commented on the relative dearth of quantitative estimates for dry forests and savannas relative to moist tropical forests (e.g. Salis et al., 2006; Williams et al., 2008), although with exceptions, such as work in the Thicket Biome of South Africa ([Mills et al., 2005], [Mills and Cowling, 2006] and [Powell, 2008]). Whilst biomass per unit area in savannas is less than tropical forests, the high rates of disturbance through fire and land clearing and their significant global extent, makes it imperative that the carbon stocks of savannas are adequately quantified and reported (Bombelli et al., 2009). This will then provide the basis for more accurate global estimates and predictive allometric equations, thereby bringing substance to the appeal of Lal (2002), namely to facilitate mobilisation of provisions of the Kyoto protocol to manage savannas for carbon sequestration benefits through maintenance of

existing woody biomass or reforestation. Lal (2002) also suggests agricultural intensification and biofuel plantations as two other approaches to increase carbon pools in savannas and drylands. However, the low rainfall and competition with other land uses limit their viability in many places (Woomer et al., 2004).

Whilst time-consuming work, determination of woody plant biomass relationships with any of a series of morphometric variables usually yields highly significant results, especially after transformation of one or both sides of the dependent and independent variables. The most commonly used independent variable from a variety of vegetation types is stem diameter or stem circumference ([Dayton, 1978], [Hofstad, 2005], [Dias et al., 2006] and [Salis et al., 2006]). Inclusion of tree height sometimes improves the relationship ([Chidumayo, 1988] and [Brown et al., 1989]), although not always (Brown et al., 1989). It is also a covariate with stem diameter. Crown diameter, area or volume have also been used as the predictor variable by some authors ([Kelly and Walker, 1977] and [Deshmukh, 1992]), but generally yield weaker regression relationships than stem circumference, and become very variable in dense vegetation where crown size is constrained ([Tietema, 1993] and [Powell, 2008]). Combinations of diameters, height and crown dimensions may provide the best predictive capacity, but are rarely worth the extra time and effort required to measure all three (Hofstad, 2005).

Within the context of the above, the objective of this study was to characterise the species dominance, biomass and carbon stocks of the woody vegetation at relatively un-impacted, potential benchmark sites, across a rainfall gradient in the savannas of the central lowveld, South Africa. We do so by field sampling to determine the vegetation composition of the tree and shrubs, followed by destructive sampling to derive allometric equations of the dominant species.

2. Study areas

The central lowveld spans approximately 11,000 km² between the Limpopo and Mpumalanga provinces of South Africa. It is characterised by a range of land use activities dominated by subsistence agriculture, private ecotourism enterprises and State conservation areas ([Shackleton, 1996] and [Pollard et al., 2003]). There is a strong rainfall gradient from the Drakensberg mountains in the west (1 200 mm p.a.) to the international border with Mozambique in the east (500 mm p.a.). Due to the combined effects of mega herbivores, fire and land clearing, the tree and shrub biomass of different land use types is highly variable in space and time ([Higgins et al., 1999] and [Shackleton and Scholes, 2000]), although there is a net negative trend in the subsistence farming areas where human population densities are over 300 persons km⁻² (Giannecchini et al., 2007).

Three localities were located along the rainfall gradient. The north–south distance between the localities is approximately 62 km. The east–west displacement is 16 km. Altitude at all these localities is approximately 550 m a.s.l. The arid locality is a 2000 ha nature reserve surrounding the Hoedspruit (HNR) airforce base (24° 20' S; 30° 57' E). The semi-arid locality, at Wits Rural Facility (WRF) (24° 30' S; 31° 06' E) covers 350 ha and is managed as a tertiary education and research facility. The mesic locality is situated in the central lowland area of Bushbuckridge Nature Reserve (BNR) (24° 51' S; 31° 05' E). Bushbuckridge Nature Reserve is approximately 4000 ha in extent, but only the central section is comparable to the other two localities with respect to geology and geomorphology, hence all work was limited to an easily definable 550 ha portion on the lowlands.

All three localities are situated on weathered granites with doleritic intrusions reaching the surface in isolated places. Typical catenal sequences are evident at all three localities. Thus, upland soils are

shallow, coarse-textured and dystrophic, whilst bottomland soils are deeper, finer-textured and more eutrophic.

Mean annual rainfall (MAR \pm SE) is the primary variable differentiating the three localities, being 484 ± 32 (n = 27) at the arid site, 651 ± 123 (n = 28) at the semi-arid site, and > 870 mm at the mesic site (MAR at Injaka (2 km west, 780 m a.s.l.) = $1161 \text{ mm} \pm 225$; n = 5). At all localities rainfall is concentrated into the summer season from October to May. The length of the rainy season increases with increasing MAR. Rain is received largely in the form of convectional thundershowers, although periods of prolonged cyclonic showers do occur.

The three localities fall into Mucina and Rutherford's (2006) broad vegetation type of Granite Lowveld dominated by members of the Mimosaceae and Combretaceae, with the former giving way to the latter along the gradient. The arid site is dominated by *Acacia nigrescens*, *A. gerrardii*, *Albizia harveyii*, *Dichrostachys cinerea*, *Combretum apiculatum*, *Sclerocarya birrea*, *Ormocarpum trichocarpum* and *Grewia* species. Mean height of the canopy is 5–6 m.

The semi-arid locality is dominated by Combretaceae species including *Terminalia sericea*, *Combretum collinum* and *C. hereroense*, with *S. birrea* and *D. cinerea* also being significant contributors to the biomass. Mean canopy height is 6–7 m.

The mesic locality is situated on the boundary between the Granite Lowveld and the Pretoriuskop Sour Bushveld vegetation types. It is dominated by taller (8–9 m), more broadleaved species than the other two sites, namely *Pterocarpus angolensis*, *Faurea saligna*, *T. sericea*, *C. collinum*, *Parinari curatellifolia* and *Dombeya rotundifolia*, along with *S. birrea* and *D. cinerea*. More details of the vegetation at each locality are provided in the Results.

Biomass of indigenous fauna at the semi-arid and mesic localities is low. The arid locality has a range of indigenous ungulates, with a mean biomass of 34 kg/ha, dominated by giraffe (30.0%), Burchell's zebra (12.5%), blue wildebeest (10.5%), impala (9.5%) and waterbuck (8.9%).

In precolonial times, the whole region was only sparsely inhabited due to the prevalence of tsetse fly and malaria. However, with commercialisation of the lowlands for cattle production, as well as land purchases by large mining companies to reserve access to mineral rights, increased settlement occurred, both on crown lands, as well as private lands as labour tenants (Pollard et al., 2003). It is to be expected that the increasing settlement density had localised impacts on the fauna and flora, but not of significant magnitude. Relics of human settlements (pot sherds, grinding stones, grain pits, etc.) are to be found within each locality indicating past human occupation, but there appear to be no macro-environmental disturbances resulting from these.

After the turn of the century all three localities were subjected to cattle ranching up until the mid 1960s or 1970s. Wild ungulates were also present during this period, but with almost no active management. The arid locality was declared a military area in 1978, and a nature reserve established as a surrounding buffer zone. Wild ungulates were reintroduced, and the area is currently managed by the South African National Defence Force. The semi-arid site became a commercial game ranch in 1968, focusing on tourism. Stumps of large trees of commercially valuable species such as *Pterocarpus angolensis* and *Combretum imberbe* are evident at the semi-arid locality, and to a lesser extent, the mesic locality. Local inhabitants say that at the semi-arid locality these species were cut out to supply a furniture factory, which may explain why the biomass per hectare at this locality is lower than at the arid locality (see Results). In 1988 most of it was converted to a research and education centre of the University of the Witwatersrand. There is little active management of the

natural habitat other than a periodic block burn conditional on fuel-load. Wild ungulate biomass is low. The mesic locality was designated as a nature reserve in 1975. The reserve was not fenced and thus experienced continuous low levels of cattle grazing, and removal of resources (thatch, fuelwood, fruits, and carving timber) by neighbouring inhabitants. The area was fenced in 1994, but some resources are still removed by the surrounding communities as there is little management or control. The reserve is burnt every one or two years, intentionally or unintentionally.

3. Methods

The woody vegetation at each study reserve was characterised by means of randomly located belt transects; 95 at the arid locality, 30 at the semi-arid locality, and 52 at the mesic locality. Transect size was 5 m × 50 m at the arid and mesic localities, and 5 m × 80 m at the semi-arid locality. Transect size differed since the density and individual stem data for the semi-arid locality were taken from Shackleton (1993).

Within each transect the following variables were measured for each woody stem irrespective of whether the plant was multi- or single-stemmed (as the number of plant individuals cannot be inferred from number of stems for many species): (1) height, (2) basal circumference at 5 cm above ground level, unless coincidental with the basal swelling, in which case the basal circumference just above the swelling was taken, and (3) species. Heights less than two meters were measured using a tape. Heights greater than two meters, but less than 4.5 m were estimated visually against a ranging rod to the nearest 10 cm. Heights greater than 4.5 m were determined via trigonometric conversion after measuring an angle to the top of the tree with an Abney level.

Biomass of each stem of the common and dominant species (with a suitable range in stem size classes available) was determined using locally derived allometric equations, either empirically during this study or for some species from previous work. In summer (February–April) fifteen to twenty stems of each of the common and dominant species at the arid (*Ormocarpum trichocarpum*), semi-arid site (*Acacia gerrardii*, *A. swazica*, *Combretum collinum*, *Dichrostachys cinerea*, and *Terminalia sericea*), and moist (*Faurea saligna*, *Pterocarpus angolensis*, and *Parinari curatellifolia*) sites were selected. The basal circumference and crown diameter (long axis and short axis) were measured. Each tree was felled with a hand-saw as close to the ground as possible. Once felled, the height of the canopy base, total height, and height of the remaining stump were recorded. The fresh mass was determined in the field for the whole stem (up to the first significant branching), leaves only, twigs (current season's growth), and wood. The leaves and twigs were stripped by hand. Subsamples of each component were oven-dried at 85 °C for 7 days to allow correction to dry mass. All masses reported are dry mass unless stated otherwise. The mean moisture content was 41.5% for wood, 51.5% for twigs and 55.0% for leaves. Biomass of *Acacia nigrescens*, *Combretum apiculatum*, *Grewia bicolor*, and *Sclerocarya birrea*, was determined using the allometric equations of Scholes (1987) from the same region. Biomass of species for which allometric equations were not available was determined using the general equation of Rutherford (1979). Carbon content was taken as 48% of dry biomass for all components, as the general mean for hardwoods (Lamlom and Savidge, 2003).

The mass data were \log_{10} transformed. A range of models were tested as the best predictors of $\log(\text{tree mass})$, including stem diameter, stem diameter², $\log(\text{stem diameter})$, stem area, stem circumference, stem circumference², $\log(\text{stem circumference})$, canopy area and tree height. Diameter and circumference provided equivalent relationships, and both provided consistently better models than tree height, canopy area or stem area. Given that stem circumference is easily measurable with a high degree of precision and does not require conversion for analysis, it, rather than stem diameter,

was used as the independent variable. Given the log transformation of mass, a double log relationship consistently provided higher r^2 values than a single log relationship, except for *P. curatellifolia*. Analysis of residuals was used to detect significant outliers. After transformation no outliers were evident.

The term microphyll is used applied loosely to the four of the nine species in the allometric analysis that are fine leaved (*A. gerrardii*, *A. swazica*, *D. cinerea* and *O. trichocarpum*) relative to the remaining five species. The maximum potential height for each species was determined as the mean height of the three tallest stems of each species from the belt transect data. Regenerative stems were taken as those with a basal circumference of less than 2 cm and not associated with a coppice stump, i.e. they were new individuals or from root stock. The same allometric equations were used, although the contribution of regenerative stems to total biomass is negligible. If coppice stumps were encountered (relatively few) the size of the original stump was recorded rather than the size of the new coppice shoots.

Significant differences in most variables were assessed using one-way ANOVA. Subsequent pairwise comparisons on significant ANOVAs used the Least Significant Difference. Size class distribution profiles were compared using a Kolmogorov–Smirnov test.

4. Results

4.1. Species composition

There were considerable dissimilarities in the species composition between the three localities (Table 1). The top three species in terms of biomass at the arid site were *Acacia nigrescens*, *Sclerocarya birrea* and *Combretum apiculatum*, which when combined contributed 13.8% of the total biomass. On a density basis the shrubby species of *Dichrostachys cinera* and *Grewia bicolor* contributed the most number of stems. At the semi-arid site the three species that contributed most to the biomass were *Sclerocarya birrea*, *Combretum collinum* and *Terminalia sericea* (11.5% combined), with *D. cinerea* and *T. sericea* contributing the most to density. At the mesic site almost one quarter of the biomass was contributed by the top three species of *Pterocarpus angolensis*, *Faurea saligna* and *Terminalia sericea*. *D. cinerea* was the species with the highest density here also. There was a decreasing proportion of the biomass in spinescent species as well as members of the Mimosaceae with increasing rainfall ($p < 0.0001$) (Fig. 1).

Table 1. The species contributing 2% or more to either the density, biomass or basal area at each locality.

Locality	Species	Density		Basal area		Biomass	
		(stems/ha)	%	(m ² /ha)	%	(t/ha)	%
Arid	<i>Acacia exuvialis</i>	130.5	2.5	0.047	0.5	0.033	0.1
	<i>Acacia nigrescens</i>	133.1	2.6	1.211	12.2	5.407	23.5
	<i>Albizia harveyii</i>	130.5	2.5	0.889	9.0	1.962	8.5

Locality	Species	Density		Basal area		Biomass	
		(stems/ha)	%	(m ² /ha)	%	(t/ha)	%
	<i>Combretum apiculatum</i>	557.9	10.8	2.058	20.8	3.683	16.0
	<i>Combretum hereroense</i>	91.4	1.8	0.242	2.4	0.410	1.8
	<i>Commiphora schimperii</i>	172.6	3.3	0.048	0.5	0.014	0.1
	<i>Dichrostachys cinerea</i>	932.6	18.0	0.580	5.9	0.500	2.2
	<i>Grewia bicolor</i>	700.6	13.5	0.467	4.7	0.366	1.6
	<i>Grewia flava</i>	452.6	8.7	0.248	2.5	0.177	0.8
	<i>Grewia flavescens</i>	212.2	4.1	0.044	0.5	0.026	0.1
	<i>Lannea stuhlmanniana</i>	13.1	0.3	0.307	3.1	0.991	4.3
	<i>Ormocarpum trichocarpum</i>	409.3	7.9	0.253	2.6	0.185	0.8
	<i>Peltophorum africanum</i>	25.3	0.5	0.230	2.3	0.427	1.9
	<i>Sclerocarya birrea</i>	16.8	0.3	1.271	12.8	4.672	20.3
	Total	3 978.5	76.8	7.88	79.8	18.85	82.0
	<i>Acacia swazica</i>	304.3	5.5	0.227	2.6	0.152	0.8
	<i>Albizia harveyii</i>	144.3	2.6	0.298	3.5	0.494	2.4
	<i>Combretum collinum</i>	292.5	5.3	1.037	12.0	3.180	15.7
	<i>Dichrostachys cinerea</i>	1227.5	22.0	0.911	10.6	0.863	4.3
Semi-arid	<i>Diospyros mespiliformis</i>	32.5	0.6	0.447	5.2	1.669	8.3
	<i>Euclea natalensis</i>	192.5	3.5	0.110	1.3	0.079	0.4
	<i>Maytenus senegalensis</i>	215.0	3.9	0.098	1.1	0.058	0.3
	<i>Philenoptera violacea</i>	41.8	0.7	0.519	6.0	2.137	10.6
	<i>Sclerocarya birrea</i>	107.5	1.9	1.348	15.6	6.223	30.7

Locality	Species	Density		Basal area		Biomass	
		(stems/ha)	%	(m ² /ha)	%	(t/ha)	%
	<i>Strychnos madagascariensis</i>	321.8	5.8	0.667	7.7	1.404	6.9
	<i>Terminalia sericea</i>	1116.8	20.1	1.462	16.9	2.135	10.6
	Total	3 996.5	71.9	7.12	82.5	18.41	91.0
	<i>Annona senegalensis</i>	223.1	1.1	0.371	2.6	0.330	0.8
	<i>Antidesma venosum</i>	1113.1	5.2	0.441	3.1	0.712	1.7
	<i>Combretum collinum</i>	793.1	3.7	1.053	7.5	3.006	7.2
	<i>Dichrostachys cinerea</i>	2896.1	13.6	0.689	4.9	0.521	1.3
	<i>Dombeya rotundifolia</i>	1059.2	5.0	0.073	0.5	0.065	0.2
	<i>Euclea natalensis</i>	584.6	2.8	0.025	0.2	0.008	–
	<i>Faurea saligna</i>	2820.0	13.3	2.193	15.6	8.910	21.5
	<i>Heteropyxis natalensis</i>	559.2	2.6	0.262	1.9	0.756	1.8
Mesic	<i>Ochna</i> sp	659.2	3.1	0.010	–	0.002	–
	<i>Parinari curatellifolia</i>	1936.9	9.1	0.775	5.5	1.433	3.5
	<i>Pavetta schumanianna</i>	1131.5	5.3	0.093	0.7	0.063	0.2
	<i>Pterocarpus angolensis</i>	326.9	1.5	2.574	18.3	9.291	22.4
	<i>Pterocarpus rotundifolius</i>	596.9	2.8	0.359	2.6	0.925	2.2
	<i>Sclerocarya birrea</i>	37.7	0.2	1.222	8.7	5.227	12.6
	<i>Strychnos madagascariensis</i>	1793.1	8.4	0.513	3.7	0.992	2.4
	<i>Terminalia sericea</i>	1999.2	9.4	1.783	12.7	5.665	13.6
	Total	18 530	87.1	12.44	88.5	37.91	91.4

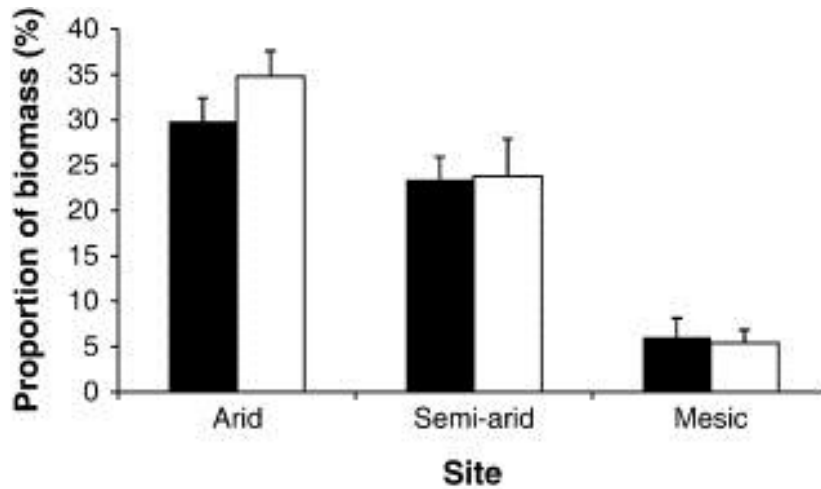


Fig. 1. Proportional contribution of spinescent species (□) and members of the *Mimosaceae* (■) to total biomass at each locality.

4.2. Species allometry

Total mass (log transformed) was strongly related to stem circumference ($p < 0.0001$) for all species examined (Table 2). The total dry mass of wood was also strongly related to stem circumference, as was the mass of the stem, and mass of branches alone, along with leaves and twigs (Table 3). The contribution of stem wood to the total mass of wood varied significantly between species, from 18% to 46%, and was positively correlated with the maximum potential height per species using the function $sq\ root(\% \text{ of total wood in stem}) = 0.0026(\text{max. pot. height}) + 4.048$ ($r^2 = 0.48$; $n = 9$; $p < 0.05$). The percentage of the total dry mass contributed by wood increased with increasing stem size (all species pooled: $r^2 = 0.11$; $p < 0.0001$; $n = 142$).

Table 2. Regression relationship of per species between log(dry mass) and stem circumference (cm) for selected dominant species in the central lowveld.

Species	log(dry mass)		log(fresh mass)	
	r^2	(kg)	r^2	(kg)
<i>A. gerrardii</i>	0.99	= 2.633 (log(circ))-2.580	0.97	= 2.628 (log(circ))-2.348
<i>A. swazica</i>	0.94	= 2.441 (log(circ))-2.423	0.94	= 2.396 (log(circ))-2.146
<i>C. collinum</i>	0.98	= 2.365 (log(circ))-2.319	0.98	= 2.362 (log(circ))-2.084
<i>D. cinerea</i>	0.96	= 2.521 (log(circ))-2.460	0.96	= 2.521 (log(circ))-2.243
<i>F. saligna</i>	0.96	= 2.606 (log(circ))-2.908	0.97	= 2.558 (log(circ))-2.550
<i>O. trichocarpum</i>	0.95	= 2.104 (log(circ))-2.116	0.96	= 2.157 (log(circ))-1.979

Species	log(dry mass)		log(fresh mass)	
	r ²	(kg)	r ²	(kg)
<i>P. curatellifolia</i>	= 0.033 (circ)–0.360	0.95	= 0.033 (circ)–0.004	0.95
<i>P. angolensis</i>	= 2.446 (log(circ))–2.545	0.97	= 2.414 (log(circ))–2.192	0.97
<i>T. sericea</i>	= 2.585 (log(circ))–2.612	0.98	= 2.608 (log(circ))–2.414	0.99

Table 3. Regression relationships between wood mass (kg) components and stem circumference (cm). (* = not significant).

Species (and max. potential height)	Log (dry mass) (kg)	r ²	Log (dry mass) (kg)	r ²
<i>A. gerrardii</i> (4.3 m)	Total wood = 2.692(log circum)–2.699	0.99	Leaves = 2.075(log circum)–2.983	0.95
	Stem = 2.330(log circum)–2.885	0.91	Twigs = 1.130(log circum)–3.111	0.38
	Branch = 2.834(log circum)–3.018	0.98		
<i>A. swazica</i> (3.6 m)	Total wood = 2.647(log circum)–2.703	0.94	Leaves = 1.747 (log(circ.))–2.753	0.85
	Stem = 2.457(log circum)–3.180	0.73	Twigs = 0.440 (log(circ.))–2.486	0.17*
	Branch = 2.726(log circum)–2.940	0.84		
<i>C. collinum</i> (8.1 m)	Total wood = 2.387(log circum)–2.404	0.97	Leaves = 2.224 (log(circ.))–3.137	0.96
	Stem = 2.052(log circum)–2.481	0.86	Twigs = 2.155 (log(circ.))–4.096	0.96
	Branch = 2.582(log circum)–2.883	0.94		
<i>D. cinerea</i> (3.1 m)	Total = 2.559(log circum)–	0.96	Leaves = 2.257 (log(circ.))–	0.94

Species (and max. potential height)	Log (dry mass) (kg)	r ²	Log (dry mass) (kg)	r ²
<i>F. saligna</i> (8.5 m)	wood	2.571	3.043	
	Stem	= 2.363(log circum)– 3.205	0.73 Twigs	= 2.014 (log(circ.))– 4.004 0.87
	Branch	= 2.641(log circum)– 2.756	0.95	
	Total wood	= 2.701(log circum)– 3.102	0.96 Leaves	= 1.834(log circum)– 2.900 0.89
	Stem	= 2.391(log circum)– 2.903	0.95 Twigs	= 1.401(log circum)– 2.971 0.70
	Branch	= 3.119(log circum)– 4.132	0.91	
<i>O. trichocarpum</i> (2.5 m)	Total wood	= 2.119(log circum)– 2.151	0.95 Leaves	= 1.855(log circum)– 3.280 0.89
	Stem	= 2.896(log circum)– 3.763	0.89 Twigs	= 1.093(log circum)– 3.625 0.39
	Branch	= 1.915(log circum)– 2.254	0.88	
<i>P. curatellifolia</i> (10.2 m)	Total wood	= 2.665(log circum)– 3.092	0.92 Leaves	= 2.102(log circum)– 3.433 0.90
	Stem	= 2.602(log circum)– 3.411	0.96 Twigs	= 2.083(log circum)– 4.160 0.90
	Branch	= 0.040(circum)–1.003	0.89	
	Total wood	= 2.443(log circum)– 2.575	0.96 Leaves	= 2.637(log circum)– 4.069 0.96
<i>P. angolensis</i> (10.2 m)	Stem	= 2.157(log circum)– 2.482	0.92 Twigs	= 2.674(log circum)– 5.151 0.93
	Branch	= 0.027(circum)–0.271	0.92	
<i>T. sericea</i> (8.4 m)	Total	= 2.687(log circum)–	0.98 Leaves	= 2.022(log circum)– 0.98

Species (and max. potential height)	Log (dry mass) (kg)	r^2	Log (dry mass) (kg)	r^2
wood	2.827		2.716	
Stem	= 2.590(log circum)- 3.391	0.81	Twigs = 1.594(log circum)- 3.313	0.82
Branch	= 2.762(log circum)- 3.054	0.97		

There was a significantly greater ratio of leaf to twig mass for microphyllous than mesophyllous species ($F = 25.5$; $d.f = 141$; $p < 0.0001$) (Fig. 2).

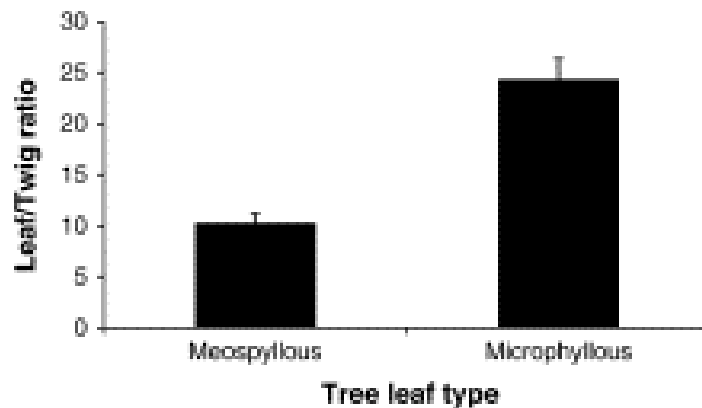


Fig. 2. Leaf mass:twig mass ratio of mesophyllous and microphyllous species.

4.3. Vegetation structure

There was a gradient of increasing density, height of canopy, basal area, biomass and carbon from the arid locality to the mesic one, although the semi-arid site was not always intermediate between the two (Table 4). The size-class distribution profile at the mesic locality was significantly different to that at the arid and semi-arid localities ($S = 0.45$; $p < 0.0001$), having a greater proportion of stems in the smallest size class, and fewer stems in the intermediate size classes (Fig. 3). The proportion of stems in the largest size classes were similar at all three sites. Although there was a tendency for the proportion of stems in a given size class at the semi-arid locality to be intermediate between the arid and mesic, the distribution profiles between the arid and semi-arid localities were not significantly different ($S = 0.06$; $p > 0.05$).

Table 4. Woody community structural characteristics at the arid, semi-arid and mesic localities (\pm SE). (Note: transect size at the semi-arid locality was almost double than that at the other two).

Variable	Locality			p
	Arid (n = 95)	Semi-arid (n = 30)	Mesic (n = 52)	
Density of all stems (no./ha)	5208 (235.1)	5583 (328.0)	21,374 (1410.6)	< 0.0001 a a b
Basal area (m ² /ha)	10.1 (0.61)	8.6 (0.90)	14.1 (0.93)	< 0.0001 a a b
Biomass (t/ha)	23.1 (2.28)	18.9 (3.67)	41.3 (4.53)	< 0.0001 a a b
Carbon (t/ha)	11.6 (1.3)	9.5 (1.8)	20.7 (2.3)	< 0.001 a a b
Volume (m ³ /ha)	52.2 (4.83)	43.5 (7.7)	94.8 (9.7)	< 0.0001 a a b
Height of tallest stem/transect (m)	6.61 (0.28)	6.69 (0.52)	8.91 (0.35)	< 0.0001 a a b

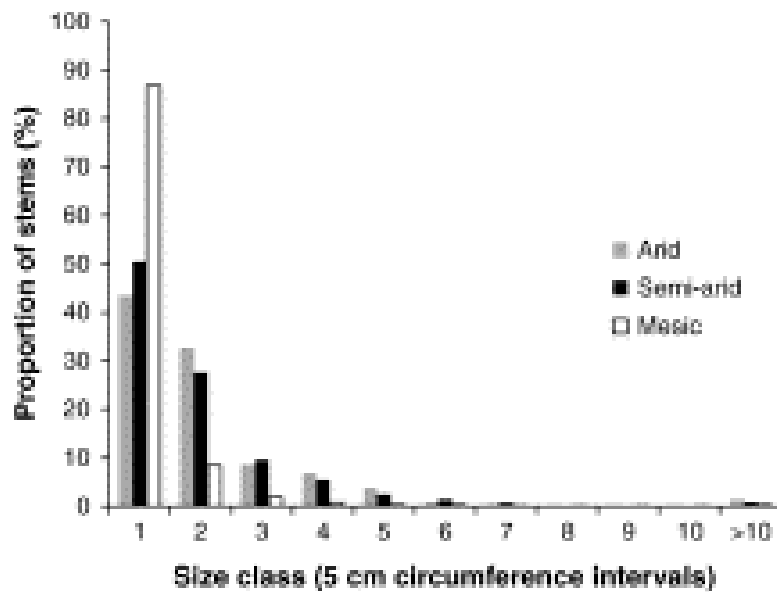


Fig. 3. Size class profiles at the arid (▣), semi-arid (■), and mesic (□) localities.

The proportion of regenerative stems differed significantly between the three localities ($F = 162.1$; $p < 0.0001$), being highest at the mesic locality, and least at the arid locality (Fig. 4). Whilst there was a strong trend of an increasing proportion of regenerative stems with increasing rainfall, the difference between the arid and semi-arid localities was not significant.

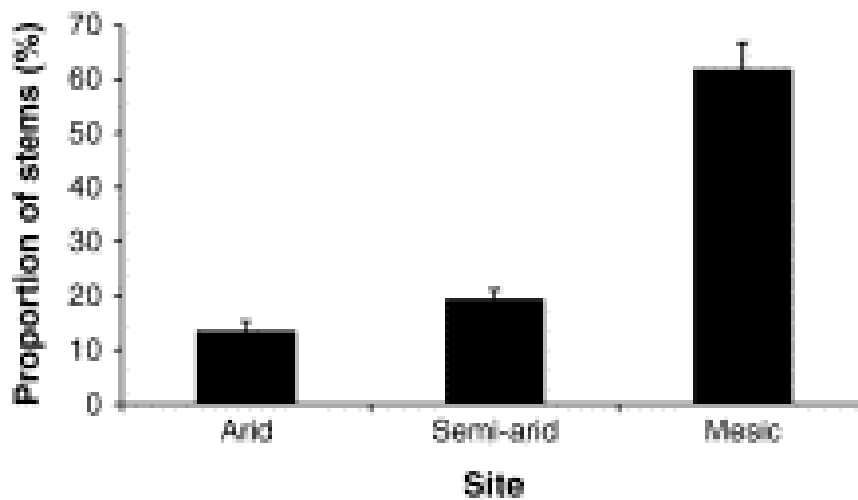


Fig. 4. Proportion of regenerative stems at each locality.

5. Discussion

Floristically, the three localities are typical of the broader vegetation types of the region, each with subcomponents differentiated largely on the basis of rainfall and topo-edaphic gradients (e.g. [Gertenbach, 1983], [Fraser et al., 1987] and [Witkowski and O'Connor, 1996]). However, several changes were evident along the gradient of increasing rainfall, including increasing woody stem density, height of the canopy, number of species, density of regenerative stems and a greater proportion of stems in small size classes. The proportion of spinescent species decreased with increasing rainfall. An important question to consider in assessing the significance of these trends, as highlighted by Witkowski and O'Connor (1996), is the degree to which changes in structure are a response to environmental gradients rather than changing species composition. Their study indicated marked changes in community physiognomy along the primary environmental gradients (mainly edaphic) after species composition was accounted for.

These trends relative to rainfall conform to other studies contrasting vegetation in different rainfall zones (e.g. Frost, 1996) as well as current understanding of savanna woody structure and dynamics (Scholes and Walker, 1993). Frost (1996) provided regressions of stand basal area and stand biomass relative to MAR for miombo woodlands. Both had a positive relationship with rainfall. However, the regression relationships he provided did not match the data from this study ($p < 0.005$). No relationship was found between density and MAR by Frost (1996) for miombo woodlands, but a trend was apparent when comparing the three intensive study localities described here.

The attractiveness of allometric relationships is vastly enhanced if a single suite of equations is applicable for more than one species for general estimates of standing woody biomass (Hofstad, 2005). At first glance at the data in Table 1 it appeared that this was unlikely. However, general relationships are evident if the smaller shrubby species (multi-stemmed species, generally less than 4 m maximum height) are considered independently from the taller tree species, summarised as $\log(\text{tree dry mass}) = 2.397(\log(\text{circ.})) - 2.441$ ($r^2 = 0.94$; $p < 0.00001$) and $\log(\text{shrub dry mass}) = 2.320(\log(\text{circ.})) - 2.30$ ($r^2 = 0.94$; $p < 0.00001$).

Since the same data from the individual species relationships were also used to determine the mean line, it is not possible to statistically test for significant differences or goodness-of-fit of the individual species lines against the mean line (Tietema, 1993). However, with respect to trees, most of the relationship attributes for each species individually are well within one standard deviation of the mean line, except *A. gerrardii* where the slope deviates by slightly more than one standard deviation, and *P. angolensis* where the intercept is also slightly greater than one standard deviation less than the mean. Similarly, for shrubs, the slope and intercept of the individual species relationships were within one standard deviation of the mean, except the intercept for *A. swazica*.

In a similar fashion Tietema (1993) found that a single regression line (“combine”) adequately represented the biomass relationships of 14 tree species in Botswana. Independent validation of his combine against species from other continents suggested that it was a robust relationship, with wide applicability for gross biomass studies. Unfortunately, it relates to fresh mass rather than dry mass. Conversion to dry mass using the moisture contents derived in our study allows comparison. Up to 60 cm circumference, the Tietema (1993) combine results in markedly higher dry masses for a given circumference than the one derived here. Above 60 cm circumference the opposite applied. Chidumayo (1988) also derived a single line to estimate fuelwood volume from stem circumference for nine species in Zambia. He too found that separate lines were necessary for shrubby understory species and larger trees. Scholes (1987) derived allometric relationships for five savanna species in the same region as this study, but their fit against the summary line derived here is poor, as they provide a significantly higher mass than the combine. The poor comparability of results from separate workers questions the general applicability of a single line for a defined region for gross biomass studies. Clearly, studies of the growth and biomass dynamics of a single species would be best accomplished with using an equation derived specifically for that species. Even for general biomass studies Tietema (1993) recommended that individual species relationships be used for the dominant species, and a summary line or combine, for the lesser species. Dayton (1978) argued that one must expect a unique set of equations for individual species, and Hofstad (2005) adds that even within a single species relationships may differ between sites, and hence should always be locally defined.

There are relatively few data from similar vegetation types against which we can compare the biomass results of this study. A number of allometry studies have been done in southern African savannas. However, most have reported the biomass of specific, individual species and few have considered the total biomass per unit area. Of those that do, the biomass per hectare report here is comparable. Williams et al. (2008) reported carbon stocks in savannas of Mozambique with comparative figures from Zimbabwe, most of which fell in the range of 16 to 26 tC/ha, whereas in our study the range is from 9.5 to 20.5 tC/ha.

Enumeration of carbon stocks is a basic step in carbon accounting and consideration of land use options and strategies to promote carbon sequestration. Benchmark sites are vital as they allow determination of deviations under different land uses. For example, Banks et al. (1996) recorded an aboveground biomass of approximately 1400 kg/ha at intensively used sites around two villages in

the semi-arid lowveld. When compared against the benchmark sites reported in this study, we can see that above ground carbon stocks at those sites have declined by over 90%, and that an additional 8000–8500 tC/ha could be restored. Inclusion of soil carbon would make these differentials even greater, and in the central lowveld are potentially larger pools than above ground (Wise et al., 2009). In mid level impacted sites Banks et al. (1996) found stocks of 1300 tC/ha, indicating an additional above ground 7700 tC/ha could be maintained under appropriate management. Precisely what constitutes appropriate management would have to be determined in consultation with local communities and farmers. However, few are likely to currently be aware of the potential for carbon credits via either reforestation or REDD+. If this was communicated to communities and farmers in such situations, some would certainly entertain the idea of management approaches to increase woody biomass, and hence carbon stocks if appropriate and efficient financing channels could be established. This will not be easy, but with supportive policies and intermediaries it is possible, whilst simultaneously delivering other biodiversity and livelihood benefits (Vella et al., 2005). Working with numerous small communities or farmers to achieve economies of scale results in high transaction costs, but the potential for real livelihood improvements whilst capturing carbon makes it worthwhile (Jindal et al., 2008), and is possible even in low biomass regions if sufficiently large parcels of land are enumerated as a means to reduce transaction costs (Wise et al., 2009). Additionally, using locally trained enumerators, as has been done in West Africa, can save the typically high costs associated with external experts (Skutsch and Ba, 2010).

In conclusion, this study provides a useful benchmark of relatively intact systems within the central lowveld against which other estimates can be compared, especially in areas experiencing noticeable loss of woody cover via human agency, fire or megaherbivores. These can then be used in calibrating the above ground carbon stocks in models of land use change. It provides the first step towards a fuller carbon inventory, which would need to include soil, litter and herbaceous carbon, although the last two are relatively small, and highly variable in response to fire, grazing and rainfall.

Acknowledgements

The bulk of the field work for this study was made possible by sponsorship from the Green Trust, for which we are grateful.

References

1 Banks, D.I., Griffin, N.J., Shackleton, C.M., Shackleton, S.E., Mavrandonis, J.M.

Wood supply and demand around two rural settlements in a semi-arid Savanna, South Africa

(1996) *Biomass and Bioenergy*, 11 (4), pp. 319-331.

2 Bombelli, A., Henry, M., Castaldi, S., Adu-Bredu, S., Arneeth, A., De Grandcourt, A., Grieco, E., (...), Valentini, R. The Sub-Saharan Africa carbon balance, an overview (2009) *Biogeosciences Discussions*, 6 (1), pp. 2085-2123.

3 Brown, S., Gillespie, A.J.R., Lugo, A.E. Biomass estimation methods for tropical forests with applications to forest inventory data (1989) *Forest Science*, 35 (4), pp. 881-902.

- 4 Chidumayo, E.N. Estimating fuelwood production and yield in regrowth dry miombo woodland in Zambia (1988) *Forest Ecology and Management*, 24 (1), pp. 59-66.
- 5 Dayton, B.F. Standing crops of dominant *Combretum* species at three browsing levels in the Kruger National Park (1978) *Koedoe*, 21, pp. 67-76.
- 6 Deshmukh, I. Estimation of wood biomass in the Jubba Valley, southern Somalia, and its application to East African rangelands (1992) *African Journal of Ecology*, 30 (2), pp. 127-136.
- 7 Dias, A.T.C., de Mattos, E.A., Vieira, S.A., Azeredo, J.V., Scarano, F.R. Aboveground biomass stock of native woodland on a Brazilian sandy coastal plain: Estimates based on the dominant tree species (2006) *Forest Ecology and Management*, 226 (1-3), pp. 364-367.
- 8 Eaton, J.M., Lawrence, D. Loss of carbon sequestration potential after several decades of shifting cultivation in the Southern Yucatán (2009) *Forest Ecology and Management*, 258 (6), pp. 949-958.
- 9 Fraser, S.W., Van Rooyen, T.H., Verster, E. Soil-plant relationships in the central Kruger National Park (1987) *Koedoe*, 30, pp. 19-34.
- 10 Frost, P.G. The ecology of miombo woodlands (1996) *The Miombo in Transition: Woodlands and Welfare in Africa*, pp. 11-57.
- 11 Gertenbach, W.P.D. Landscapes of the Kruger National Park. (1983) *Koedoe*, 26, pp. 9-121.
- 12 Giannecchini, M., Twine, W., Vogel, C. Land-cover change and human-environment interactions in a rural cultural landscape in South Africa (2007) *Geographical Journal*, 173 (1), pp. 26-42.
- 13 Higgins, S.I., Shackleton, C.M., Robinson, E.R. Changes in woody community structure and composition under contrasting land use systems in a semi-arid savanna, South Africa (1999) *Journal of Biogeography*, 26 (3), pp. 619-627.
- 14 Hofstad, O. Review of biomass and volume functions for individual trees and shrubs in Southeast Africa (2005) *Journal of Tropical Forest Science*, 17 (1), pp. 151-162.
- 15 Jindal, R., Swallow, B., Kerr, J. Forestry-based carbon sequestration projects in Africa: Potential benefits and challenges (2008) *Natural Resources Forum*, 32 (2), pp. 116-130.
- 16 Kelly, R.D., Walker, B.H. The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia (1977) *Journal of Ecology*, 64, pp. 553-576.
- 17 Lal, R. Carbon sequestration in dryland ecosystems of West Asia and North Africa (2002) *Land Degradation and Development*, 13 (1), pp. 45-59.
- 18 Lamtom, S.H., Savidge, R.A. A reassessment of carbon content in wood: Variation within and between 41 North American species (2003) *Biomass and Bioenergy*, 25 (4), pp. 381-388.
- 19 Miles, L., Kapos, V. Reducing greenhouse gas emissions from deforestation and forest degradation: Global land-use implications (2008) *Science*, 320 (5882), pp. 1454-1455.

- 20 Mills, A.J., Cowling, R.M. Rate of carbon sequestration at two thicket restoration sites in the Eastern Cape, South Africa (2006) *Restoration Ecology*, 14 (1), pp. 38-49.
- 21 Mills, A.J., Cowling, R.M., Fey, M.V., Kerley, G.I.H., Donaldson, J.S., Lechmere-Oertel, R.G., Sigwela, A.M., (...), Rundel, P. Effects of goat pastoralism on ecosystem carbon storage in semiarid thicket, Eastern Cape, South Africa (2005) *Austral Ecology*, 30 (7), pp. 797-804.
- 22 The vegetation of South Africa, Lesotho and Swaziland (2006) *Strelitzia*, 19, pp. 1-807. L. Mucina, M.C. Rutherford (Eds.)
- 23 Pollard, S.R., Shackleton, C.M., Carruthers, J. Beyond the fence: people and the lowveld landscape (2003) *The Kruger Experience: Ecology and Management of Savanna Heterogeneity*, pp. 422-446. Island Press, California, Du Toit, H. Biggs, G. Mills, B. Naiman, K. Rogers (Eds.)
- 24 Powell, M.J. (2008) , p. 144. Restoration of degraded subtropical thickets in the Baviaanskloof Megareserve, South Africa: the role of carbon stocks and *Portulacaria afra* survivorship. MSc Thesis, Rhodes University, Grahamstown
- 25 Rutherford, M.C. Above-ground biomass subdivisions in woody species of the savanna ecosystem project study area, Nylsvley (1979) *South African National Scientific Programmes Report* 36. CSIR, Pretoria
- 26 Salis, S.M., Assis, M.A., Mattos, P.P., Pião, A.C.S. Estimating the aboveground biomass and wood volume of savanna woodlands in Brazil's Pantanal wetlands based on allometric correlations (2006) *Forest Ecology and Management*, 228 (1-3), pp. 61-68.
- 27 Scholes, R.J. (1987) Responses of three semi-arid savannas on contrasting soils to the removal of the woody component. PhD Thesis, University of the Witwatersrand, Johannesburg
- 28 Scholes, R.J., Hall, D.O. The carbon budget of tropical savannas, woodlands and grasslands (1996) *Global Change: Effects on Coniferous Forests and Grasslands*, pp. 69-99. John Wiley & Sons, Chichester, UK, A.I. Breyer, D.O. Hall, J.M. Melillo, G.I. Agren (Eds.)
- 29 Scholes, R.J., Walker, B.H. An African savanna: synthesis of the Nylsvley study (1993) *An African savanna: synthesis of the Nylsvley study*, pp. 306. ISBN: 0521419719
- 30 Shackleton, C.M. Fuelwood harvesting and sustainable utilisation in a communal grazing land and protected area of the Eastern Transvaal lowveld (1993) *Biological Conservation*, 63 (3), pp. 247-254.
- 31 Shackleton, C.M. Potential stimulation of local rural economies by harvesting secondary products: A case study of the central Transvaal Lowveld, South Africa (1996) *Ambio*, 25 (1), pp. 33-38.
- 32 Shackleton, C.M., Scholes, R.J. Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park (2000) *Koedoe*, 43 (1), pp. 75-81.
- 33 Skutsch, M.M., Ba, L. Crediting carbon in dry forests: The potential for community forest management in West Africa (2010) *Forest Policy and Economics*, 12 (4), pp. 264-270.

- 34 Savanna modelling for global change (1991) *Biology International*, 24. O.T. Solbrig, J.C. Menaut, M. Mentis, H.H. Shugart, P. Stott, D. Wigston (Eds.)
- 35 Tietema, T. Biomass determination of fuelwood trees and bushes of Botswana, Southern Africa (1993) *Forest Ecology and Management*, 60 (3-4), pp. 257-269.
- 36 Vella, K.J., Williams, R.J., Walker, D.H., Smajgl, A., Kirschbaum, M.U.F., Greiner, R. Viewpoint: Social and economic dimensions of involving savanna communities in carbon management systems (2005) *Australian Journal of Botany*, 53 (7), pp. 741-747.
- 37 Williams, M., Ryan, C.M., Rees, R.M., Sambane, E., Fernando, J., Grace, J. Carbon sequestration and biodiversity of re-growing miombo woodlands in Mozambique (2008) *Forest Ecology and Management*, 254 (2), pp. 145-155.
- 38 Wise, R.M., von Maltitz, G.P., Scholes, R.J. (B.), Elphinstone, C., Koen, R. Estimating carbon in savanna ecosystems: rational distribution of effort (2009) *Mitigation and Adaptation Strategies for Global Change*, pp. 1-26.
- 39 Witkowski, E.T.F., O'Connor, T.G. Topo-edaphic, floristic and physiognomic gradients of woody plants in a semi-arid African savanna woodland (1996) *Vegetatio*, 124 (1), pp. 9-23.
- 40 Woomer, P.L., Touré, A., Sall, M. Carbon stocks in Senegal's Sahel Transition Zone (2004) *Journal of Arid Environments*, 59 (3), pp. 499-510.