TREE BIOMASS IN SOUTH AFRICAN SAVANNAS:
FLYING OVER, HUGGING, AND DESTROYING TREES TO SAVE THEM

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Abstract

The abstracts for the three primary chapters (after the introduction in Chapter 1) are:

**Chapter 2.** The distribution of woody biomass in savannas reflects spatial patterns fundamental to ecosystem processes, such as water flow, competition, and herbivory, and is a key contributor to savanna ecosystem services, such as fuelwood supply. While total precipitation sets an upper bound on savanna woody biomass, the extent to which substrate and terrain constrain trees and shrubs below this maximum remains poorly understood, often occluded by local-scale disturbances such as fire and trampling. Here we investigate the role of hillslope topography and soil properties in controlling woody plant aboveground biomass (AGB) in Kruger National Park, South Africa. Large-area sampling with airborne Light Detection and Ranging (LiDAR) provided a means to average across local-scale disturbances, revealing an unexpectedly linear relationship between AGB and hillslope-position on basalts, where biomass levels were lowest on crests, and linearly increased toward streams ($R^2 = 0.91$). The observed pattern was different on granite substrates, where AGB exhibited a strongly non-linear relationship with hillslope position: AGB was high on crests, decreased midslope, and then increased near stream channels ($R^2 = 0.87$). Overall, we observed 5-to-8-fold lower AGB on clayey, basalt-derived soil than on granites, and we suggest this is due to herbivore-fire interactions rather than lower hydraulic conductivity or clay shrinkage/swelling, as previously hypothesized. By mapping AGB within and outside fire and herbivore exclosures, we found that basalt-derived soils support tenfold higher AGB in the absence of fire and herbivory, suggesting high clay content alone is not a proximal limitation on
AGB. Understanding how fire and herbivory contribute to AGB heterogeneity is critical to predicting future savanna carbon storage under a changing climate.

**Chapter 3.** Tree biomass is an integrated measure of net growth and is critical for understanding, monitoring and modeling ecosystem functions. Despite the importance of accurately measuring tree biomass, several fundamental barriers preclude direct measurement at large spatial scales, including the fact that trees must be felled to be weighed, and that even modestly sized trees are challenging to maneuver once felled. Allometric methods allow for estimation of tree mass using structural characteristics, such as trunk diameter. Savanna trees present additional challenges, including limited available allometry and a prevalence of multi-stemmed trees. Here we collected airborne LiDAR data over a pristine semi-arid savanna adjacent to the Kruger National Park, South Africa and then harvested and weighed woody plant biomass at the plot scale to provide a standard against which field and airborne estimation methods could be compared. We found for an existing airborne LiDAR method that half of the total error was due to averaging canopy height at the plot scale. This error was eliminated by instead measuring maximum height and crown area of individual trees from LiDAR data using an object-based method to identify individual tree crowns and estimate their biomass. The object-based method approached the accuracy of field allometry at both the tree and plot levels, and roughly doubled the accuracy compared to existing airborne methods. We found allometric error accounted for 22-30% of the total error in airborne biomass estimates at the plot scale. Airborne methods also gave more accurate predictions at the plot-level than field methods based on diameter-only allometry. These results provide a
novel comparison of field and airborne biomass estimates using harvested plots and advance the role of LiDAR remote sensing in savanna ecosystems.

**Chapter 4.** Tree biomass is both a fundamental state variable of ecosystems and the critical parameter in effectively monitoring aboveground carbon stocks. Destructively harvesting and weighing biomass is labor intensive, expensive, and prohibited in protected areas. Thus one of the largest sources of error in non-destructively estimating forest biomass is the selection of an allometric model. This is particularly problematic in African savanna woodlands, where limited availability of allometry, small sample sizes, and lack of harvested large trees make it unclear whether species-specific allometries are more accurate than generic models or significantly different from each other. It also remains unclear whether variation in growth form or wood specific gravity (ρ) is the principal cause of biomass differences among savanna species. Here we constructed ten species-specific allometric models from 714 destructively harvested stems in savanna woodland near Kruger National Park, South Africa. Three of the four most common woody species had fits significantly different (p < 0.05) from one another, with the highest species curve (*Acacia nigrescens*) more than twice the biomass of the lowest (*Sclerocarya birrea*) even for moderately sized trees (D = 10 cm). We then compared the form factors (taper) of each species by dividing mass by ρ and cylindrical volume, showing most species are in the range of $F = 0.78-0.80$ without significant variation between most species. These results suggest there are both statistically significant and ecologically substantial differences between the allometries of common savanna species, and that variation in wood density is the primary source of biomass differences between these species.
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The doctoral dissertation is the capstone of years of individual research, carried out by a lone intellectual wolf, climbing the endless steps of an ivory tower in pursuit of knowledge and, if all goes well, carving out another step engraved with his or her initials. Or so some claim. In truth, or at least in my case, a dissertation is a team effort directly and indirectly supported by a network of colleagues, friends, and family, rivaling the craftiest of think tanks, the funniest of late-night TV show hosts, and more chocolaty than cookies pulled straight out of the oven by the Oracle herself (Wachowski, 1999).

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Chapter 1.

Introduction

Upon receiving his wife’s inheritance and retiring soon thereafter, the Flemish physician Johannes Baptista van Helmont turned to chemistry and performed the first experimental measurement of tree biomass in the written record (published in 1648, four years after his death):

“… I took an earthen pot and in it placed 200 pounds of earth which had been dried out in an oven. This I moistened with rain water, and in it I planted a shoot of willow which weighed five pounds. When five years had passed the tree which grew from it weighed 169 pounds and about three ounces… Finally I dried out the earth in the pot once more, and found the same 200 pounds, less about two ounces. Thus 164 pounds of wood, bark, and roots had arisen from water alone.” - J. B. van Helmont (1648)

Indeed, measuring changes in tree mass over time and inferring mechanisms of growth stretches back at least 350 years. Helmont did not recognize the contribution of carbon dioxide to the mass of the tree, claiming instead the willow tree “had arisen from water alone” (even though he also coincidentally discovered carbon dioxide from burning charcoal). While this does not diminish the experiment’s importance that the majority of a tree does not come from the soil, this idea is far older than Helmont, dating back to at least 400 A.D. when Rufinus of Aquileia translated the eighth book of the Greek Clementine Recognitions into Latin (Howe 1965): “By manifest fact and example let us
prove that nothing is supplied to seeds from the substance of the earth, but that they are entirely derived from the element of water and the spirit (spiritus) that is in it.” The example refers to a thought experiment quite similar to Helmont’s actual experiment, whereby three tons of earth will yield another three tons of wheat and barley after several years, without any loss of earth.

With the ancient Greeks and renaissance Flemish on our side, it is perhaps surprising that accurately estimating biomass remains an issue in the 21st century. This in part due to a shift in the scale of the problem at hand, from measuring a single tree to the more challenging estimation of the mass of an entire forest stand, motivated initially by the rise of managed forests as early as the 16th century in China, Japan, and Germany. The first forestry schools were established in 1825, with German forester and educator Sir Dietrich Brandis developing techniques around 1860 to measure teak volume, rate of growth, and rate of harvest in Burma (Negi 1991, Rajan 1998). Brandis was also influential in the beginning of the sustainable forestry movement and mentored several pivotal foresters, including Carl Schenck and the first U.S. chief foresters, Franklin Hough (1876-1883) and Gifford Pinchot (1898-1910). Hough and Pinchot were alarmed by decreasing timber stocks and environmental damage caused by deforestation, and felt it was the role of the government to preserve forests. Thus by 1900 the needs of forest management were already growing and with it, a body of technical literature detailing the science of forest measurement, such as equations estimating merchantable tree volume using paraboloids (Schenck 1905). These relations would later become the foundation of modern biomass allometry, which relate destructively harvested mass, typically
aboveground dried woody biomass (AGB), to structural characteristics, such as diameter and height.

Beyond simply maximizing harvestable timber, the challenges in biomass estimation again shifted in the 20th century to understanding the ecological mechanisms and controls over plant growth in natural ecosystems. Knowledge of a tree’s mass serves as an integrated measure of net growth, minus losses from partial mortality. However, estimating the mass of a natural forest is a different beast than estimating that of a plantation, not only in the diversity of flora and fauna but also in topography, soil, climate, and other environmental conditions. A hectare of a tropical forest in Amazonia, for example, typically includes hundreds of species (Baker et al. 2004). Even if species composition were constant over large distances, forest canopy structure varies depending on precipitation, light competition, nutrient availability, temperature, length of growing season, dispersal mechanisms, herbivory, and disturbances. The relative importance of these factors in determining tree structure varies from biome to biome.

The study of savanna vegetation structure and function was well underway by the early 20th century, with parallel studies of savannas in Australia, South America, Africa, and North America converging on traits common to all savannas. Apart from the central concept that they are communities of mixed trees and grasses, savannas do differ from forests and grasslands in several key respects. Tropical savannas of Australia, South America, and Africa are characterized by hot-wet summers with heavy rainfall events and warm-dry winters with rare frosts, whereas temperate savannas, such as oak savannas in the North American Great Plains, withstand sub-freezing temperatures (Bray 1955, Ovington et al. 1963). Another unique characteristic of all savannas is that primary
production, hydrology, and nutrient cycling are strongly, but differentially, mediated by both woody plants and grasses (Scholes and Walker 1993). However, a savanna is not simply a linear combination of grasslands and forests because tree-grass interactions asymmetrically favor established trees over grasses yet established grasses are favored over tree seedlings.

Frequent grass fires are intrinsic to savannas, occurring annually in tropical wet savannas or once every ten years or longer in dry savannas (Trollope and Potgieter 1986). Grass fires also amplify tree-grass dynamics, knocking back saplings just as they have overcome competition with grass, but having little effect on established trees (Bond and Keeley 2005a). Fire can also lead to fast nutrient mineralization, otherwise microbial decomposition of tree leaf litter is very slow (3-5 years) and one year for grass litter (Scholes and Walker 1993). Mineralization and nutrient uptake operate in a pulsed, non-continuous manner due to the discrete rainfall events that occur in dry savannas. Therefore water plays a central role in controlling the duration of growth and nutrient uptake, with savannas alternating between water limitation and nutrient limitation. Although multiple nutrient limitation occurs and primary production will respond to fertilization with water, nitrogen, or phosphorus, even in infertile savannas, the response is limited, as observed in other nutrient poor ecosystems (Chapin III et al. 1986, Scholes and Walker 1993).

The first vegetation map of Africa depicting savanna distribution was released in 1959 (Keay), showing that savannas occupy about 40% of Africa and 20% of global land surface (depending on how one classifies savannas). Rutherford (1979) published a foundational set of biomass allometry for African savanna woody species, specifically for
the use of ecological studies rather than forestry. However, the paper only reported the model coefficients and $R^2$, omitting the sample size, standard error, and, importantly, the range of diameters used to create the allometry. Over the following decade, additional destructive biomass harvests were conducted in South African savannas to improve the biomass allometry available for quantifying savanna energy and carbon budgets (Scholes 1988, Goodman 1990). In 2011 Alecia Nickless combined the Scholes and Goodman datasets, refit allometric equations, and published a new set of 17 species-specific and two generic allometries (Nickless et al. 2011), which to my knowledge contains the current and most robust South African allometry to date.

Understanding the links between spatially explicit vegetation patterns and savanna ecosystem function is critical aspect of savanna ecology explored in this dissertation. This was in part the impetus behind the collaboration between the Carnegie Department of Global Ecology and South African National Parks (SANParks), culminating in the Carnegie Airborne Observatory (CAO) flying Kruger National Park (KNP), South Africa, in April 2008. The CAO is an airborne remote sensing payload comprised of two boresight-aligned instruments, a Light Detection and Ranging (LiDAR) imaging system and a Visible-to-Near Infrared imaging spectrometer (VNIR). The LiDAR uses an infrared laser to generate three-dimensional maps of tree canopy structure at 1.12 m laser spot spacing, and the VNIR is a passive sensor mapping canopy reflectance at the same horizontal resolution. During the 2008 campaign the CAO collected 700 km² of both LiDAR and VNIR data. KNP was selected as the study site for a few reasons: long-term experimental herbivore and fire exclosure (~40 yr old); the lack of any appreciable land use change within the park for almost a century; the park’s large
size (~2 Mha) encompasses many climatic, geologic, and topographic gradients and savanna subtypes. Few studies of woody AGB have previously been conducted in the park, although recently Nickless et al. (2011) estimated mean AGB inside KNP at 23 Mg ha\(^{-1}\) near Skukuza inside the park.

I have organized the remainder of the dissertation into three chapters. In Chapter 2, I investigate the spatially explicit patterns of savanna biomass at landscape and regional scales, using a combination of airborne LiDAR and estimated AGB at the plot level using the Nickless (2011) allometry. The data indicated at landscape scales a non-linear relationship between mean AGB and hillslope-position on granites (\(R^2 = 0.87\)), as expected from the literature and field work, whereas the data revealed an unexpectedly linear relationship between AGB and hillslope-position on basalts, opposite in direction to that found on the granites (\(R^2 = 0.91\)). At the regional scale AGB spatially coincided with known geologic boundaries, and, importantly, the AGB variation between parent materials far outweighed that due to variation in precipitation between sites.

In Chapter 3 I investigated first how removing the “middleman” of field allometry improves airborne LiDAR AGB estimates. Here airborne LiDAR data were collected over a pristine semi-arid savanna adjacent to the Kruger National Park, South Africa, then all woody plant biomass within 30 plots (3,068 stems) was harvested and weighed to provide a standard against which field and airborne AGB estimation methods were compared. We found for an existing airborne LiDAR method that half of the total error was due to averaging canopy height at the plot scale. This error was eliminated by instead measuring maximum height and crown area of individual trees from LiDAR data using an object-based method to identify individual tree crowns and estimate their biomass.
The object-based method approached the accuracy of field allometry at both the tree and plot levels, and roughly doubled the accuracy compared to existing airborne methods. These results provide a novel comparison of field and airborne biomass estimates using harvested plots and advance the role of LiDAR remote sensing in savanna ecosystems.

In Chapter 4 I make use of the harvest results again to develop species-specific biomass relationships to answer three questions. I first address whether the allometries of common woody species in KNP are both statistically and substantially different from one another. I found three of the four most common woody species had significantly different fits (p < 0.05), with the highest curve (Acacia nigrescens) more than twice the biomass of the lowest (Sclerocarya birrea). Importantly, the most common woody species in KNP have wide enough differences in allometry curves to warrant species-specific allometry to minimize allometric error, although the generic model presented in Chapter 3 is sufficient for smaller trees (D < 10cm) if a species-mean wood specific gravity (ρ) is available. The second question of Chapter 4 asked whether differences between species allometrics were primarily due to ρ or form factor (taper)? This question also has implications for how to best predict species from remote sensing: if ρ is the dominant factor, then species prediction will have to rely primarily only on hyperspectral data, whereas LiDAR is better suited to estimating F. These results demonstrate wood density was the primary difference in biomass allometries between these savanna woody plant species.

In summary the ability to map spatially explicit patterns of woody biomass to environmental gradients, disturbances, and land-use history provides unique insight into any ecosystem, but savannas particularly benefit from the use of airborne LiDAR to capture the high structural heterogeneity. By combining directly measured tree mass with
airborne remote sensing, this study uniquely demonstrates an object-based LiDAR method that approaches the accuracy of field estimates of aboveground biomass. This opens the door for further research in understanding how topographic, edaphic, and other environmental gradients correlate with biomass patterns, as well as permitting up-scaling to global maps of savanna biomass using satellite-derived data.
Chapter 2.

Topo-edaphic controls over woody plant biomass in South African savannas

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Abstract

The distribution of woody biomass in savannas reflects spatial patterns fundamental to ecosystem processes, such as water flow, competition, and herbivory, and is a key contributor to savanna ecosystem services, such as fuelwood supply. While total precipitation sets an upper bound on savanna woody biomass, the extent to which substrate and terrain constrain trees and shrubs below this maximum remains poorly understood, often occluded by local-scale disturbances such as fire and trampling. Here we investigate the role of hillslope topography and soil properties in controlling woody plant aboveground biomass (AGB) in Kruger National Park, South Africa. Large-area sampling with airborne Light Detection and Ranging (LiDAR) provided a means to average across local-scale disturbances, revealing an unexpectedly linear relationship between AGB and hillslope-position on basalts, where biomass levels were lowest on crests, and linearly increased toward streams ($R^2 = 0.91$). The observed pattern was different on granite substrates, where AGB exhibited a strongly non-linear relationship with hillslope position: AGB was high on crests, decreased midslope, and then increased near stream channels ($R^2 = 0.87$). Overall, we observed 5-to-8-fold lower AGB on clayey, basalt-derived soil than on granites, and we suggest this is due to herbivore-fire interactions rather than lower hydraulic conductivity or clay shrinkage/swelling, as previously hypothesized. By mapping AGB within and outside fire and herbivore exclosures, we found that basalt-derived soils support tenfold higher AGB in the absence of fire and herbivory, suggesting high clay content alone is not a proximal limitation on AGB. Understanding how fire and herbivory contribute to AGB heterogeneity is critical to predicting future savanna carbon storage under a changing climate.
Key words: LiDAR, Carnegie Airborne Observatory, Kruger National Park, carbon storage, topographic controls

1 Introduction

In savannas the spatial pattern of woody plants is driven by climate, topography, soils, competition, herbivory, and fire over a wide range of scales (Skarpe 1992, Scholes and Archer 1997). Coughenour and Ellis (1993) investigated these potential drivers and the scales at which they operate over a large area of Kenyan savannas (9,000 km$^2$), spanning a rainfall gradient equivalent to that of the Sahel. They found that woody canopy cover was correlated primarily with rainfall at regional scales, tree height to drainage water subsidies at hillslope scales, and species composition to landscape-scale properties, such as substrate and elevation. Environmental drivers of vegetation patterns operate and interact across a range of scales in savannas, although the relative importance of each is poorly understood.

A related issue is the scale at which vegetation patchiness is observed in savannas (Wiegand et al. 2006, Moustakas et al. 2009, Levick and Rogers 2011). Spatial patterns of savanna trees and shrubs begin at the scale of the plants themselves, with canopies typically 3-6 m both in height and crown diameter and mean canopy cover of 10-40%, although trees over 10 m and much higher canopy cover are not uncommon (Scholes and Walker 1993). Clumping in the form of multi-stemmed shrubs and trees is common in savannas, hypothesized as a defense mechanism against fire (Scholes and Archer 1997). Tree-grass interactions are another key driver of savanna heterogeneity at the local scale (Belsky 1994, Archer 1995, Scholes and Archer 1997, Sankaran et al. 2004). According
to niche separation models, grass fine roots absorb the majority of soil moisture near the surface, leaving what water infiltrates below for woody plants (Belsky 1994, Sankaran et al. 2004). Soil particle size, or texture, is a primary determinant of infiltration rates and water retention, and in many savannas where soil organic matter content is low, it plays an even more dominant role (Scholes and Walker 1993, Brady and Weil 1996). Although finer textured soils generally have higher soil water retention, when they dry out the small amount of moisture is more tightly bound to clay-sized particles than in sand, resulting in low water availability to plants (Williams 1983, Brady and Weil 1996, Fensham R.J. and Fairfax 2007). Conversely, sandy surface soils can preclude capillary movement, with the consequence that deep moisture reserves are less diminished during drought than fine-textured surface soils (Alizai and Hulbert 1970).

Downslope variation in these soil properties leads to topographic controls over savanna vegetation patterns. The term catena has long been used to describe hydrologically mediated soil and vegetation interactions associated with hillslope position (Milne 1936, Ruhe 1960). Many studies have characterized savanna catenas in granite landscapes, describing their formation and ecological significance (Milne 1936, Munnik et al. 1990, Venter and Scholes 2003); less is known about basaltic savanna catenas, where slopes <1° more resemble plains more than hills. Savanna geomorphologists find that the dominant flow regime (throughflow vs. overland flow) varies between substrate types (Venter and Scholes 2003, Khomo 2008). During rainfall events on sandy soils, there is vertical infiltration and subsequent downslope movement of water in the subsoil (throughflow), which transports clay and cations to the footslope. In Kruger National Park, South Africa, the granitic landscapes exhibit sandy crests
(<15% clay) but duplex soils on the footslopes (sandy A horizon overlaying a 20-35% clay B horizon) (Venter and Scholes 2003), hypothesized to be the result of throughflow transport of clay particles in soil solution acting over 1-10 million year timescales (Khomo 2008, Khomo et al. 2011). From crest to footslope, there is a downslope decline in clay content until an abrupt transition occurs, called the seepline, at which point throughflow is forced to the surface by the high clay content of the B horizons (Bern et al. 2011). In contrast, basaltic substrates weather to soils with much higher clay contents (35-60%) throughout the entire profile, making them likely dominated by overland flow (Venter and Scholes 2003).

These soil properties associated with hillslope position have wide ranging effects on vegetation patterns. Coarse-textured crest soils allow trees access to throughflow, providing a competitive edge over grasses (Morrison 1948, Walter 1971, Scholes and Archer 1997). Conversely, downslope transport and accumulation of salts on granitic footslopes can result in impervious sodic B horizons and seasonal waterlogging, keeping woody cover low (Venter and Scholes 2003). Van Langevelde et al. (2003) modeled results suggested trees can occur on sandy soils for a lower range of rainfall than on clayey soils due to higher percolation rates, and observations show trees can establish under drier conditions on sandy soils than on clayey soils. These edaphic and hydrologic properties are hypothesized to explain low woody plant AGB on basalt-derived soils.

At the regional scale (10-100 km) variation in geology is a primary correlate with vegetation patterns. In the savannas of Kruger National Park, homogenous regions of granitic substrate may stretch for 50 km, only to transition to basalt over a few tens of meters. These savannas typically have higher woody cover on the granitic sandy soils
than the basaltic clayey soils, suggesting higher water availability on granites outweighs the cost of lower nutrient concentrations. However, it has been shown that disturbance is often the proximal cause of this lower woody cover, with higher nutrient concentrations in basaltic soils leading to increased grass production, higher fire intensity, and suppressed recruitment of woody plants (Trollope and Potgieter 1986, Scholes and Walker 1993, Bond and Keeley 2005b). Elephants and other mega-herbivores damaging bark severely increases fire vulnerability of large trees (Eckhardt et al. 2000). While a full investigation into fire and herbivory controls is outside the scope of this study, we recognize topo-edaphic controls do not operate in a vacuum devoid of these disturbances and address potential implications below.

In light of high variance in AGB at the plot scale, it remains logistically challenging to conduct field studies with sample sizes sufficiently large to capture topo-edaphic trends in AGB. Airborne LiDAR (Light Detection and Ranging) measures vegetation structure at the sub-canopy scale (e.g. 1 m resolution) while covering large geographic areas (e.g. >100 km$^2$ per day). Airborne LiDAR has been used extensively for mapping AGB in tropical and temperate forests (Lefsky et al. 1999, Drake et al. 2002, Asner 2009b), and in this study we apply this approach to African savannas. Here we focus on topographic and soil controls over the spatial distribution of savanna woody biomass. We utilized the large areal coverage afforded by airborne LiDAR to test the following hypotheses: 1) Biomass follows a topographic pattern of high values on crests, low on midslopes, and high near streams on both granites and basalts. 2) AGB is more sensitive to geologic parent material than to precipitation within the KNP range of 400-800 mm$^{-1}$ yr. 3) AGB is lower on basalts relative to granite due to herbivore-fire
interactions rather than clay shrinkage/swelling or lower hydraulic conductivity. These hypotheses are aimed at elucidating the importance of topography and soil properties, relative to climate and disturbance regimes, in controlling the spatial distribution of AGB in savannas.

2 Methods

2.1 Study sites

KNP (24°S, 31.5°E) is located in eastern South Africa, spanning 360 km N-S and 70 km E-W. Eight study landscapes were flown in 2008 covering 70,978 ha of KNP’s major substrate, topographic, and climatic gradients (Fig. 1). KNP is roughly split into equal halves of granite in the west and basalt in the east, with granite substrates weathered to sandy, nutrient-poor soils and basalts weathered to clay-rich, primarily smectitic soils (Venter and Scholes 2003). The granitic landscapes exhibit distinct catena patterns, despite the shallow nature of the hillslopes (3-5°). In contrast the southern basalts are flatter (0.5-1°) and exhibit a linear increase in clay content from 30% to 60% from crest to toeslope (Venter and Scholes 2003). Gabbro intrusions are scattered throughout the park and are also weathered to clay-rich, smectitic soils.

The climate of KNP is primarily semi-arid, with mean annual temperature and precipitation (MAP) of 22 °C and 550 mm yr⁻¹, respectively, and an average potential evaporation of 7 mm/day (du Toit et al. 2003). The precipitation is primarily rainfall, which ranges from ~300-500 mm yr⁻¹ in the north to 500-700 mm yr⁻¹ in the south, and a similar east-west gradient in the south. Granite catena soil depth and seepline distance
from crest are known to increase with MAP in KNP (Olbrich 1984, Chappel 1993, Khomo 2008, Levick et al. 2010).

The woody species commonly associated with the southern granites (e.g. Skukuza) consist of broadleaf *Combretum spp.* on crests, little woody cover on the backslope, and a sparse cover of fineleaf *Acacia* shrubs and stunted trees on the toeslope. The southern basalts support sparse woody cover of *Acacia* spp. and large marula (*Sclerocarya birrea*), although it is largely unknown whether a vegetation catena pattern similar to that on the granites exists here. The northern Shingwedzi and Roan landscapes are dominated by *Colophospermum mopane*. Few studies of woody AGB have previously been conducted in the park, although studies in savannas of similar vegetation and climate estimate KNP woody AGB to range from 10–40 Mg ha$^{-1}$ (Scholes and Walker 1993, du Toit et al. 2003). Most recently Nickless et al. (2011) estimated AGB at 22.9 Mg/ha using a 4 ha field plot in KNP on a granite substrate near Skukuza.

Herbivore and fire exclosures, setup and maintained by KNP researchers, were utilized to investigate AGB in the absence of fire and herbivory. The experimental design and history of the exclosures are described by Levick et al. (2009), Trollope et al. (2008), and Asner et al. (2009). The two exclosures included here are those located within the airborne study landscapes of Pretoriuskop and Lower sabie and had treatment durations of 36 yr and 34 yr, respectively.

### 2.2 Field biomass estimation

Field inventories were conducted within the extent of the LiDAR data during the overflights in April-May 2008 to inform and validate airborne estimates of AGB. Field
plots (n=124) of equal size (30 m diameter, 0.07 ha) were established for LiDAR-biomass calibration. Riparian woodlands adjacent to major rivers (Strahler stream order ~5 and greater) were not included in this study as they require a separate calibration and represent less than 2% of KNP land area. Biomass along smaller streams and drainage lines was included the study. The center of each field plot was recorded using hand-held, differentially corrected GPS receivers (GeoXT Trimble Inc., GS50 Leica Geosystems Inc.) to enable accurate registration of field-estimated AGB to airborne LiDAR data. Within each plot, basal stem diameter (10 cm above basal swelling), height, and species were recorded for all woody stems greater than 5 cm diameter and 1.5 m height.

An allometric equation specific to South African trees (Eq. 1, Appendix A) developed by Nickless et al. (2011) was used to estimate dry, woody stem biomass from stem diameter. This generalized equation was trained using 443 harvested stems of the dominant broadleaf species commonly found in KNP and performed well when fit to the harvest data ($R^2 = 0.98$, MSE = 0.12 (ln(kg))²). We chose this generalized equation over species-specific equations because many of the stems in our inventory data exceed the maximum diameter of each species-specific equation. Consequently, the species-specific equations inadequately capture variation in large tree biomass, such as stem rot, root/shoot/leaf allocation, sapwood/heartwood composition, and branch fall. Additionally, the large sample size of the broadleaf equation is eight to ten times higher than the sample size of any single species-specific equation. The stem masses were then summed over the plot and divided by plot area to arrive at a plot-level estimate of dry, aboveground woody biomass density. Appendix A gives further details of allometry methods.
2.3 Airborne biomass calibration

In April-May of 2008, the Carnegie Airborne Observatory (CAO) collected over 700 km$^2$ of discrete-return LiDAR data at a pulse repetition frequency of 50 kHz to generate three-dimensional maps of tree canopy structure at 1.12 m laser spot spacing (for the aircraft altitude flown at 2,000 m). Flights were planned with 100% repeat coverage and therefore LiDAR point density averaged two points per 1.12 m spot. LiDAR spatial errors were less than 0.20 m vertically and 0.36 m horizontally (Asner et al. 2007, Asner et al. 2009). A vegetation height map, where each 1.12 m pixel represents the canopy height above ground (m), was computed from the LiDAR point cloud by subtracting a ground DEM (classified from LiDAR last return elevation) from a canopy surface DEM (first return elevation). This vegetation height map was then used to calculate the following plot-level LiDAR metrics. Plot top-of-canopy height, $H$, is computed as the mean of all 564 pixel height values within each 30 m diameter plot circle centered at each GPS location. A height threshold identical to that used in the field (less than 1.5 m) masked out grass and ground misclassified as vegetation. Plot canopy cover (CC) is computed as the number of pixels >1.5 m in height divided by 564 (total pixels inside a plot). A total of 124 upland field plots were used to train the LiDAR-biomass regression models.

We utilized a proven LiDAR-biomass regression method to produce AGB maps from LiDAR data, although we tested a variety of plot-level LiDAR metrics to see which best predicts savanna AGB. These included top-of-canopy height ($H$), canopy cover (CC), and metrics based on weighted averages of the vertical canopy profile, such as Mean Canopy Profile Height (MCH) and Quadratic Mean Canopy Profile Height.
Top-of-canopy height outperformed measures of vertical canopy profile (e.g. MCH, QMCH) because the finer resolution (1.15 m) affords more precise height estimates for small, open canopies, which are otherwise artificially reduced by the larger kernel sizes (e.g. 5 m) required by MCH or QMCH (Lefsky et al. 1999). The final predictor variable, HxCC, multiplied top-of-canopy height by CC to account for the variability in canopy cover in these systems; a comparison of the three top-performing metrics (H, CC, H×CC) is provided in Appendix B, Figs. S1a-c. The single predictor variable HxCC was selected as the final LiDAR metric based on best goodness-of-fit, lowest uncertainty, and most parsimonious (Figs. 2a-c). The HxCC metric is also ecologically relevant, as it is roughly proportional to wood volume. The best fit was linear; more complex models were tested, such as log-log and multivariate regressions using H, CC, H×CC, but none of the more complex models improved goodness-of-fit (R²) or predictive uncertainty (RMSE, CV).

The final regression models (Figs. 2a-c) were trained on data stratified by the three dominant woody species associations found in the park: mixed Combretum spp., marula and Acacia spp., and mopane. Species with higher wood density have steeper model slopes, whereas those with large crown areas relative to AGB have shallower model slopes, such as Sclerocarya birrea and multi-stemmed Combretum apiculatum. K-fold cross-validation using k=3 was performed to estimate predictive uncertainty (RMSE) and bias for each model. Maps of AGB were created by applying the regression models (Figs. 2a-c) to LiDAR vegetation height maps.

2.4 Regional analysis and landscape modeling
To study edaphic and hillslope morphological controls over AGB, regional maps of geological and soil classes were acquired from the South African National Park Service (Venter and Scholes 2003). For the hillslope-scale studies, terrain elevation at 1 m horizontal resolution was acquired from ground digital elevation maps (DEM) derived from the CAO LiDAR data. A relative elevation map (REM) was computed using the LiDAR DEM as input to the ArcGIS Hydrology Toolbox (ArcMap 9.2 ESRI Inc.), and the difference between the elevation at each pixel and the elevation of the nearest stream is defined here as Elevation Above Stream (EAS). All AGB statistics were performed in R and uncertainty is reported as mean ± 2SE (standard error of the mean).

3 Results

3.1 Hillslope and regional variation in biomass

On granitic substrate AGB was highly spatially correlated with hillslope position. Of the topo-edaphic variables tested, EAS was the most strongly correlated with AGB. At the original scale of AGB prediction (0.07 ha), slope, profile convexity, and other morphologic variables were poorly correlated with AGB, yet they were increasingly correlated at the larger spatial scale used for subsequent landscape modeling (0.5 ha). LiDAR estimates of ground elevation and slope found the granitic hillslopes to be shallow to moderately undulating (0.6° – 4.8° slope, 95% CI of natural landscape variance), with even shallower gradients on the basalts (0.5° – 2.1° slope, 95% CI). Figure 3 illustrates the strong correlation of EAS to AGB on the Skukuza granite landscape. Here a clear, nonlinear AGB pattern emerged as a function of EAS, with high AGB along stream corridors (34.1 ± 1.4 Mg ha⁻¹ (2xSE) at 0-1 m above nearest stream),
then declining to $17.7 \pm 0.5$ Mg ha$^{-1}$ on footslopes before increasing again to $26.8 \pm 0.8$ Mg ha$^{-1}$ on crests. A fourth-order polynomial was the most parsimonious model fit to mean AGB and achieved a coefficient of determination of $R^2 = 0.87$ using EAS as the sole independent variable. A model of this same form was also tested on the raw AGB estimates (not means), but it accounted for less variance in AGB ($R^2 = 0.11$) due to high AGB variability at the plot scale (27 m) from other factors (e.g. fire history, herbivory, stream order), uncertainty in the LiDAR-AGB calibration, and natural variance in peak crest heights.

The above analysis was also conducted on basalt near Lower Sabie (Fig. 3d). AGB followed a linear decline from $8.1 \pm 0.2$ Mg ha$^{-1}$ near streams down to $4.1 \pm 0.2$ Mg ha$^{-1}$ at the crest. Higher order functions of EAS did not improve goodness-of-fit nor reduce AGB standard error. Basalt mean AGB was $6.5 \pm 0.06$ Mg ha$^{-1}$, nearly a factor of four lower than on the granites. The linear model using relative elevation alone accounted for 91% of the variance in mean AGB at the hillslope scale, yet, as on the granites, relative elevation accounted for much less AGB variance at the plot-scale ($R^2 = 0.0018$).

At the regional scale clear AGB transitions were observed along geologic boundaries. Several flight polygons contained boundaries between geologic substrates (Fig. 4), affording comparison of AGB between substrates while controlling for precipitation. The mean AGB ($\pm 2SE$) and 5-95% percentile ranges for each of these and all other flight polygons are shown in Table 1. AGB drops by over a factor of three when crossing from granite to basalt or gabbro in both the southern and northern landscapes.

3.2 Biomass sensitivity analysis
To assess the relative influence of topographic and edaphic variables on AGB, landscape models were developed to enable a biomass sensitivity analysis. The landscape models were created using LiDAR-derived AGB as the response variable and the following predictor variables: ground elevation above sea level, slope, profile convexity, plan convexity, aspect, topographic wetness index (TWI), elevation above nearest stream (REM), distance to nearest stream, Strahler stream order, and flow accumulation. A simple one-at-a-time (OAT) screening (Fig. 5) was conducted to observe the first-order sensitivity of AGB to these factors. Absolute elevation had the highest AGB sensitivity on both granite and basalt substrates, followed by slope and relative elevation. Strong linear sensitivity to relative elevation on basalt and weak linear sensitivity on granite are to be expected, given the patterns observed at the hillslope scale in Fig. 3. Consequently, stream distance also had high AGB sensitivity on the gradual basaltic slopes, where stream distance strongly co-varies with EAS and slope.

AGB sensitivity continued to decrease with flow accumulation, profile convexity, and stream order. However, AGB sensitivity to stream order was underestimated because the highest order streams (5-6) were excluded by the 95% CI range selection and AGB varies nonlinearly with stream order. Aspect, topographic wetness index, and flow accumulation had low biomass sensitivity and were excluded from the final model. Several factors with low sensitivity in the OAT analysis were included in the final model due to non-linear effects that, when modeled below, increase the factor’s AGB sensitivity (such as with relative elevation on granite). Figure 5 shows the KNP biomass map resulting from applying the final landscape models across the entirety of the park, allowing visualization of how topo-edaphic factors influence AGB.
One of the limitations of OAT analysis is an inability to capture interactions between factors. To investigate these effects, AGB and each landscape variable was plotted against all other variables for n = 82,503 samples (AGB predictions at 0.5 ha scale) (Fig. 6). All pairings initially started with linear models, but the most parsimonious polynomial model was selected if it considerably reduced residual error and improved goodness-of-fit to the raw data. EAS and distance to stream had third degree effects on AGB, similar in shape to those observed at the hillslope scale (Fig. 3). Stream order was quadratic due to rapidly increasing AGB along higher order streams. Precipitation was also best modeled using a quadratic term to capture low AGB at MAP extremes (450 and 650 mm yr$^{-1}$) but higher mean AGB at intermediate MAP (550 mm yr$^{-1}$). Absolute ground elevation was also best related to AGB using a quadratic relationship, although this is most likely due to the strong co-variance of elevation with precipitation in this region ($R^2 = 0.65$). Including these five non-linearities in multivariate landscape models increased total AGB variance explained by 50% (from $R^2 = 0.10$ to $R^2 = 0.15$ at the 0.5 ha scale). Table S1 (Appendix C) lists these models for each substrate type.

3.3 Park-wide biomass

In order to provide a baseline for park management to detect future change in AGB (e.g. due to woody encroachment, mega-herbivore impacts, etc.), we estimated total woody AGB in KNP to be 53.8 Gg dry matter, or equivalently a park-wide mean AGB density of 28.3 Mg ha$^{-1}$. This estimate excludes woodlands along riparian corridors, which account for ~2-4% of the park’s area. Park-wide total biomass was estimated by multiplying the land area of each land system from Venter and Scholes (2003) by our
corresponding mean landscape AGB estimated from LiDAR (Table 1). Dividing by the area of KNP (~1.9 Mha) yields park-wide mean AGB.

4 Discussion

4.1 Hillslope geomorphologic controls over biomass

The gradual nature of basalt slopes (<1° mean terrain gradient), typically hundreds of meters if not kilometers in length, along with generally sparse woody cover (~5%), make it difficult in the field to quantify spatial variation in AGB on basals. Yet with LiDAR measurements, we observe double the AGB on toeslopes relative to crests on basals (Fig. 3e), with a strong, linear negative relationship between AGB and hillslope position. This AGB gradient is likely the result of high A horizon clay content (30-60%) along the entirety of the slope (Venter and Scholes 2003), leading to predominantly overland flow and accumulation of water downslope, as well as potentially shallower soils on basaltic crests. This stands in contrast to the coarse-sandy granite A horizons, which permit higher infiltration rates and subsoil throughflow on crests. Although a concomitant CEC increase with clay content from basalt crest to toeslope was observed by Venter (2003), phosphorous and micronutrient concentrations (K, Ca, Mg) were relatively constant (N content not available), indicating soil nutrients do not follow the same catena pattern observed in clay content and AGB.

Although the linear relationship between hillslope position and AGB on basals can be interpreted as a catena pattern, it is different in shape and magnitude relative to the granite catenas. Apart from an overall higher mean AGB on granites, the primary distinction in granite catena shape is a dip in AGB on footslopes, with 50% higher AGB
on crests and 90% higher along streams (Fig. 3e). The mean seepline location of 7 m
EAS identified by Levick et al. (2010) in the Skukuza granitic landscape coincides with
our lowest mean AGB (17.7 ± 0.5 Mg ha\(^{-1}\)) (Fig. 3e). The soil properties downslope of
the seepline, namely B horizons with 20-30% clay and hardpan commonly near the
surface of these Solonzetic soils, likely account for the lower AGB on footslopes relative
to crests. Termite bioturbation of sandy crest soils may also increase hydraulic
conductivity and concentration of soil nutrients, thereby accentuating the difference
between crest and footslope AGB (Scholes and Archer 1997). Recent work has found that
termite mounds are primarily found on sandy crests, with the lower extent of mounds
coinciding with the seepline (Levick et al. 2010).

4.2 Regional controls over biomass

At the regional scale precipitation sets an upper bound for potential woody cover
in African semi-arid savannas, with soil and disturbance regimes determining the extent
to which this potential is realized (Sankaran et al. 2005). In KNP east-west and north-
south rainfall gradients have been hypothesized to be largely responsible for regional
variation in woody cover (du Toit et al. 2003). Yet here we observed several sharp
transitions in AGB which follow geologic boundaries (Fig. 4) that occur over short
distances (<1 km) where there is negligible variation in MAP, allowing us to control for
rainfall while comparing AGB between substrate types. Multiple study landscapes
spanning the KNP rainfall gradient permit a factorial analysis of rainfall and substrate
effects on AGB.

At low rainfall (MAP of 450 mm yr\(^{-1}\)), we observe both very high and low AGB
in the Lower Sabie region of the park (Fig. 4b). The portion overlying sedimentary shale
carries a high mean landscape AGB (82.1 ± 5.4 Mg ha$^{-1}$, averaged over 916 ha), which drops by over two orders of magnitude on basalt substrate (6.5 ± 0.12 Mg ha$^{-1}$, averaged over 6,010 ha) over a distance of a few hundred meters. The shales weather to Solonetzig duplex soils, although here the A horizon has a fine or medium sandy texture vs. Skukuza’s granite-derived, coarse sandy A horizon (Venter and Scholes 2003). The edaphic causes underlying the high AGB observed on these shales require further investigation. The second landscape at low precipitation is Shingwedzi in northern KNP (Fig. 4), where we find the same relative difference in AGB between granite and basalt (3-4 times higher on granites) as that found in southern KNP.

On the high end of the precipitation gradient (650 mm yr$^{-1}$), mean AGB on Pretoriuskop granites is 27% lower than on Skukuza granites, which is consistent with other studies attributing this westward decrease in woody cover to higher precipitation, grass biomass, and fire intensity (Trollope and Potgieter 1986, du Toit et al. 2003). However, the Pretoriuskop CAO data also reveal the discontinuity in AGB between the primary granite substrate and a gabbro intrusion (Fig. 4a), with a seven-fold drop in AGB from 21.3 ± 0.14 Mg ha$^{-1}$ on granite to 3.3 ± 0.08 Mg ha$^{-1}$ on gabbro. The gabbro portion weathers to smectitic clays similar to that found on basalts (Venter and Scholes 2003), and indeed AGB is similar between Pretoriuskop’s gabbro (3.3 ± 0.08 Mg ha$^{-1}$) and Lower Sabie’s basalts (6.5 ± 0.12 Mg ha$^{-1}$), despite being on opposite ends of the KNP rainfall gradient.

4.3 Topo-edaphic controls in the context of fire and herbivory
Several hypotheses suggest the basalt-derived soils are a proximal constraint on woody vegetation, including high clay content in the A horizon preventing adequate infiltration, shrinking/swelling of smectitic clays tearing roots, or higher nutrient concentrations allowing grasses to outcompete woody plants more than on granites (Scholes and Archer 1997, Venter and Scholes 2003). However, the idea that any of these effects are a proximal limitation to woody plant AGB is contradicted by our results from the Makhohlola experimental herbivore and fire exclosure, located in a KNP basalt landscape (Trollope et al. 2008, Levick et al. 2009). Mean AGB is more than ten-fold higher inside the exclosure (36.9 ± 7.1 Mg ha\(^{-1}\) vs. 2.7 ± 0.5 Mg ha\(^{-1}\) in and out, respectively).

Higher AGB inside the exclosure demonstrates that these basalt-derived soils are capable of supporting AGB higher than what is observed on granites, in the absence of fire and herbivory (consistent with higher phosphorus and micronutrient availability). Another exclosure of similar age on a granite substrate with lower herbivore carrying capacity and slightly lower fire intensity near Pretoriuskop (Trollope et al. 2008) showed no significant difference in AGB inside and outside the exclosure (P = 0.45, n = 500, 22.0 ± 1.2 Mg ha\(^{-1}\) inside and 22.7 ± 1.3 Mg ha\(^{-1}\) outside), suggesting AGB on granite substrates is less affected by fire and herbivory. While a detailed analysis of AGB effects from excluding herbivory and fire is outside the scope of this study, these results demonstrate fire-herbivore interactions play a critical role in down-regulating AGB on basalts, and that edaphic mechanisms alone cannot account for lower AGB on basaltic landscapes.

5 Summary
In savanna ecosystems with heterogeneity at multiple spatial scales, airborne LiDAR provides the large-area measurements needed to reveal woody vegetation patterns otherwise obscured by local variance in AGB. We found the relationship between biomass and hillslope position different both in shape and direction between parent materials, with a negative linear trend on basalts (low AGB on crests increasing downslope), in contrast to the predicted pattern found on granites, with high AGB on crests, low AGB on backslopes, and high AGB near streams. We hypothesize subsoil throughflow accounts for higher AGB on granitic crests, whereas overland flow dominates basalt landscapes, allowing water accumulation downslope to subsidize woody plant growth hindered by frequent grass fires and large ungulate populations.

At regional scales climate sets an upper bound on AGB, yet we found AGB is more sensitive to parent material than to precipitation within Kruger’s semi-arid MAP gradient (400-800 mm⁻¹ yr), with large differences in mean AGB occurring over short distances that coincide with geologic boundaries. By mapping AGB within and outside fire and herbivore exclosures, we found that basalt-derived soils can support tenfold higher AGB in the absence of fire and herbivory, suggesting high clay content alone is not a proximal limitation on AGB. Understanding how fire and herbivory contribute to AGB heterogeneity is critical to predicting future savanna carbon storage under a changing climate, as well as understanding how fuelwood resources are limited or enhanced by the landscape.
Appendices

Appendix A: Stem allometry methods

Stem biomass was estimated from field-measured stem diameter using the following broad-leafed generalized equation from Nickless et al. (2011):

$$\text{AGB} = e^{-3.47} D_s^{2.83} \times e^{0.12}$$  \hspace{1cm} \text{(Nickless et al. 2011)} \hspace{1cm} \text{Eq. (1)}$$

where AGB is aboveground woody plant dry mass (kg) and $D_s$ is basal stem diameter (cm). This regression ($R^2 = 0.98$, $n=443$, MSE = 0.12 (ln(kg))^2) was calibrated using broadleaf species commonly found in southern KNP: *Combretum apiculatum*, *Sclerocarya birrea*, *Terminalia sericea*, *Spirostachys africana*, *Euclea divinorum*, and other broad-leafed species (Nickless et al. 2011). For multi-stemmed trees, biomass was calculated separately for each stem’s diameter and then summed. Solving for AGB by taking the natural exponential of the original log-log regression derived by Nickless et al. results in an under-prediction of stem biomass because least-squares regression assumes the response variable (AGB) is normally distributed, when in fact it is log-normally distributed (Beauchamp and Olson 1973). To account for this we multiply by the correction factor $\text{CF} = e^{\frac{\sigma^2}{2}}$ to arrive at Eq (1), where $\sigma^2$ is the mean square error (MSE) in log form from Nickless et al. (2011).

We chose this generalized equation over species-specific equations because many of the stems in our inventory data exceed the diameter of the largest stem used to construct the species-specific allometry. Consequently, the species-specific equations inadequately capture variation in large tree biomass, such as stem rot, root/shoot/leaf allocation, sapwood/heartwood composition, and branch fall. Additionally, the large
sample size of the broadleaf equation is eight to ten times higher than any single species-specific equation, leading to lower predictive RMSE. For stems with diameter exceeding the 33 cm limit of Nickless’s generic broadleaf allometry, we used a generalized hardwood equation (Jenkins et al. 2003) for temperate oaks and hard maples with similar specific gravity and form factors:

\[
\text{AGB}_{\text{jenkins}} = e^{-2.01} DBH^{2.43} \times e^{\frac{(0.236)^2}{2}}
\]  

(Jenkins et al. 2003) Eq. (2)

where DBH is diameter (cm) at breast height (n=485, \(d_{\text{max}} = 230 \text{ cm}\)).

For the northern landscapes dominated by *Colophospermum mopane* shrub savanna, the species-specific equation substantially improved AGB to airborne-LiDAR metrics (Figure 2f) and was used in place of Eqn 1 for stems of this species (also with correction factor):

\[
\text{AGB}_{\text{mopane}} = e^{-2.77} DBH^{2.49} \times e^{\frac{(0.263)^2}{2}}
\]  

(Nickless et al. 2011) Eq. (3)
Appendix B: LiDAR-biomass calibration curves using only height or canopy cover

**Fig. S1** Comparison of biomass calibration curves using height (H), canopy cover (CC), and HxCC as predictor variables. All 101 field plots from southern KNP across a range of dominant woody species were used to compare these three predictors. An additional 23 plots from northern KNP are dominated by *C. mopane* with significantly different morphology and stand densities than southern KNP, and thus received a separate calibration curve (Fig. 2c). Log-log and multivariate regressions using H, CC, HxCC were also tested, but none improved goodness-of-fit ($R^2$) or predictive performance (SEE, CV) compared to these linear fits.
Appendix C: Landscape modeling results

Table S1 Landscape models describing the relation of AGB to seven landscape factors at 0.5 ha resolution. Area = the fraction of KNP covered by each model type, µ = mean of n CAO AGB estimates at 0.5 ha/pixel, all other columns are model results. Polynomial terms up to 4th-order were tested for each factor to maximize goodness-of-fit while minimizing the number of terms and the standard error. Shale is a constant because only a small area of homogenous vegetation structure (*A. harveyi* thickenets) was flown by CAO, insufficient in size for landscape modeling.

<table>
<thead>
<tr>
<th>Model Type</th>
<th>Area (%)</th>
<th>µ ± 2SE (Mg ha⁻¹)</th>
<th>RMSE (Mg ha⁻¹)</th>
<th>CV</th>
<th>Adj-R²</th>
<th>n (pixels)</th>
<th>Landscape Model Formulaᵃ</th>
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<tr>
<td>1 Granite – Comb/Acacia</td>
<td>30%</td>
<td>24.7 ± 0.06</td>
<td>16.7</td>
<td>0.68</td>
<td>0.148</td>
<td>82,503</td>
<td>B=143.6-0.5654r+0.08934r²-0.002818r³-0.3387d+0.0003409d²-2.549s+33.65c-0.1222p+0.0001157p²-0.003492t-2.235m+0.6113m²</td>
</tr>
<tr>
<td>2 Basalt – Acacia</td>
<td>19%</td>
<td>6.5 ± 0.06</td>
<td>6.3</td>
<td>0.97</td>
<td>0.149</td>
<td>15,243</td>
<td>B=-24.09+0.3967r+0.2014d-0.0003d²+1.278s-0.00645t</td>
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<tr>
<td>3 Granite – C.mopane</td>
<td>25%</td>
<td>51.6 ± 0.44</td>
<td>35.8</td>
<td>0.69</td>
<td>0.118</td>
<td>7,453</td>
<td>B=835.9+3.730r-0.5329r²+0.01467r³-11.86d+0.01802d²+3.547s+160.3c+5.429p-0.006301p²-0.04384t-0.3154m+1.499m²</td>
</tr>
<tr>
<td>4 Basalt – C.mopane</td>
<td>16%</td>
<td>17.9 ± 0.24</td>
<td>22.9</td>
<td>1.28</td>
<td>0.327</td>
<td>13,370</td>
<td>B=-19.33-11.54r+11.66r²-1.527r³-1.345d+7.348s+0.2078p-15.33m+3.33m²</td>
</tr>
<tr>
<td>5 Rhyolite</td>
<td>7%</td>
<td>8.8 ± 0.14</td>
<td>7.9</td>
<td>0.89</td>
<td>0.253</td>
<td>4,282</td>
<td>B=18.19-0.8432r+0.06936r²-0.0014999r³-0.02544d+1.822s-27.37c-0.02435p-0.008515t+2.470m-0.3632m²</td>
</tr>
<tr>
<td>6 Shale</td>
<td>4%</td>
<td>82.1 ± 0.86</td>
<td>31.5</td>
<td>0.38</td>
<td>0.145</td>
<td>1,557</td>
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<tr>
<td>TOTAL (park mean)</td>
<td>100%</td>
<td>28.3 ± 0.06</td>
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ᵃ Multivariate, non-linear models for predicting AGB using landscape-only variables at 0.5 ha scale. Variable legend: B = aboveground wood biomass (Mg ha⁻¹), r = elevation
above nearest stream (m), \(d\) = elevation above sea level (m), \(s\) = slope (deg), \(c\) = profile curvature (deg m\(^{-1}\)), \(p\) = precipitation (mm/yr), \(t\) = stream distance (m), and \(m\) = Strahler stream order of nearest stream

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<th>Geo</th>
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<th>Landscape 5% - 95% quantile (Mg ha$^{-1}$)</th>
<th>Area flown (ha)</th>
</tr>
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<tr>
<td>1</td>
<td>Pretoriuskop</td>
<td>G</td>
<td>20.0 ± 0.2</td>
<td>2.6 – 49.7</td>
<td>18,453</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ga</td>
<td>3.4 ± 0.2</td>
<td>1.5 – 10.0</td>
<td>1,404</td>
</tr>
<tr>
<td>2</td>
<td>Skukuza</td>
<td>G</td>
<td>27.5 ± 0.2</td>
<td>7.2 – 63.9</td>
<td>18,860</td>
</tr>
<tr>
<td>3</td>
<td>Sabie</td>
<td>G</td>
<td>36.8 ± 0.4</td>
<td>12.7 – 66.5</td>
<td>3,603</td>
</tr>
<tr>
<td>4</td>
<td>Lower Sabie</td>
<td>B</td>
<td>6.0 ± 0.1</td>
<td>2.1 – 17.1</td>
<td>6,011</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>9.4 ± 0.3</td>
<td>2.3 – 28.5</td>
<td>2,436</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>82.5 ± 1.6</td>
<td>26.7 – 135.6</td>
<td>844</td>
</tr>
<tr>
<td>5</td>
<td>Landuse 1</td>
<td>G</td>
<td>28.9 ± 0.6</td>
<td>7.0 – 65.5</td>
<td>2,296</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ga</td>
<td>15.0 ± 0.5</td>
<td>6.1 – 36.3</td>
<td>1,093</td>
</tr>
<tr>
<td>6</td>
<td>Landuse 2</td>
<td>G</td>
<td>21.7 ± 0.3</td>
<td>6.8 – 43.8</td>
<td>3,074</td>
</tr>
<tr>
<td>7</td>
<td>Shingwedzi</td>
<td>G</td>
<td>53.3 ± 0.8</td>
<td>14.3 – 122.4</td>
<td>4,139</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>31.3 ± 1.1</td>
<td>10.2 – 110.9</td>
<td>2,671</td>
</tr>
<tr>
<td>8</td>
<td>Roan</td>
<td>B</td>
<td>10.1 ± 0.1</td>
<td>8.1 – 16.3</td>
<td>4,543</td>
</tr>
</tbody>
</table>

a Geology: G = granite, Ga = gabbro, B = basalt, S = shale, R = rhyolite

b Mean AGB +/- 2 x standard error of the mean

c Landscape-scale AGB variance expressed as 5% to 95% quantiles

d Area flown. Note the number of AGB samples = 2 x area flown (each AGB pixel is 0.5 ha)
Fig. 1 Study site locations and geology. Numbers correspond to site ID in Table 1. Zw = Zimbabwe, MZ = Mozambique, KNP = Kruger National Park
Fig. 2 Model calibration and cross-validation to predict AGB using airborne LiDAR. Points represent calibration field plots. Three models were trained according to dominant woody species: (a) mixed broadleaf (*Combretum apiculatum*, *Combretum collinum*) and fineleaf (*Acacia nigrescens*, *Dichrostachys cinerea*) savanna (b) *Acacia* spp. and marula (*Sclerocarya birrea*) savanna (c) mopane (*Colophospermum mopane*) savanna. (d-f) Observed AGB vs. predicted AGB with test RMSE and coefficient of variation (CV) estimated using k-fold cross-validation (k = 3).
Fig. 3 Spatially explicit correlation of elevation above nearest stream (a,c) to LiDAR-estimated AGB (b,d) for granite (Skukuza, top row) and basalt (Lower Sabie, bottom row). Each point in the graph (e) represents the mean of all biomass pixel values (0.07 ha resolution) within a one meter bin of elevation for the extents shown in b,d. Error bars are 2× standard error of the mean. Note increase in AGB on granitic crests above the seepline (~7 m), whereas mean AGB on basalts exhibits a linear decrease in AGB for all elevation gain above nearest stream. Solid curve is the granite, best-fit polynomial model of (fourth order) with $R^2 = 0.87$ and dashed line is the substrate best-fit model ($R^2 = 0.91$). Note the basalt error bars are drawn but are smaller than the point icons.
Fig. 4 LiDAR-derived AGB overlaying topographic hillshade for reference for four landscapes: a) Pretoriuskop b) Lower Sabie c) Skukuza d) Shingwedzi e) Mean landscape AGB (+/- 2SE) across substrate and precipitation gradients
Fig. 5 Biomass sensitivity to landscape factors: a simple one-at-a-time (OAT) screening to observe the first-order, additive response of AGB to an initial set of landscape factors. Factors shown are DEM = ground elevation above sea level, precip = precipitation, slp = slope, REM = Relative Elevation Model (height above nearest stream), strDist = distance to nearest stream, flwAcc = stream flow accumulation, proC = profile convexity, strOrder = stream Order, asp = aspect, TWI = topographic wetness index
Fig. 6 Interactions between biomass and landscape factors. Top row indicates correlation of LiDAR-derived AGB to landscape variables for n = 82,503 CAO biomass pixels (0.5 ha/pixel) on southern granite substrate. All other rows indicate interactions between landscape factors. Blue intensity indicates point density of the raw data. Curves are the most parsimonious models fit to the raw data. Circles are median values sampled at set intervals to visualize underlying patterns in the raw data (blue). Numbers in lower-left half are $R^2$ for the model curve shown in the corresponding scatter plot, and stars indicate statistical significance (** $p < 0.01$, *** $p < 0.001$) but not necessarily ecological relevance. Landscape factors shown are: elevation above sea level (m), slope (deg), precipitation (mm/yr), distance from nearest stream (m), relative elevation model (height above nearest stream) (m), stream order, and profile curvature (positive values are convex) (deg/m).
Chapter 3.

Harvesting tree biomass at the stand-level to assess the accuracy of field and airborne biomass estimation in savannas

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Abstract

Tree biomass is an integrated measure of net growth and is critical for understanding, monitoring and modeling ecosystem functions. Despite the importance of accurately measuring tree biomass, several fundamental barriers preclude direct measurement at large spatial scales, including the fact that trees must be felled to be weighed, and that even modestly sized trees are challenging to maneuver once felled. Allometric methods allow for estimation of tree mass using structural characteristics, such as trunk diameter. Savanna trees present additional challenges, including limited available allometry and a prevalence of multi-stemmed trees. Here we collected airborne LiDAR data over a pristine semi-arid savanna adjacent to the Kruger National Park, South Africa and then harvested and weighed woody plant biomass at the plot scale to provide a standard against which field and airborne estimation methods could be compared. We found for an existing airborne LiDAR method that half of the total error was due to averaging canopy height at the plot scale. This error was eliminated by instead measuring maximum height and crown area of individual trees from LiDAR data using an object-based method to identify individual tree crowns and estimate their biomass. The object-based method approached the accuracy of field allometry at both the tree and plot levels, and roughly doubled the accuracy compared to existing airborne methods. We found allometric error accounted for 22-30% of the total error in airborne biomass estimates at the plot scale. Airborne methods also gave more accurate predictions at the plot-level than field methods based on diameter-only allometry. These results provide a novel comparison of field and airborne biomass estimates using harvested plots and advance the role of LiDAR remote sensing in savanna ecosystems.
Key words: carbon stocks, Carnegie Airborne Observatory, destructive harvest, LiDAR, object-based, tree-level, Kruger, South Africa

Introduction

Knowledge of a tree’s mass enables quantification of the ecosystem services it may provide, such as fuelwood, edible fruit, and the sequestration of greenhouse gases. Mass is also a measure of net growth integrated over time, and observing changes in the spatial distribution of biomass over climatic and topographic gradients can reveal environmental controls over tree growth (Clark et al. 1998, Houghton et al. 2001, de Castilho et al. 2006). Similarly, repeated measurements of biomass over time allow for estimation of growth rates of trees or tree stands (Whittaker et al. 1974, DeLucia et al. 1999, Houghton 2005). Despite the benefits of accurately measuring woody plant biomass, several fundamental barriers preclude the direct measurement of biomass across any substantial spatial scale in natural environments: the plants must be felled to be weighed; even modestly sized trees are challenging to maneuver once felled; and a substantial belowground mass fraction remains unmeasured.

Methods aiming to estimate biomass using non-destructive measurements of structural characteristics, such as stem diameter and height, are referred to as allometric approaches (Whittaker and Marks 1975, Cannell 1984, Brown et al. 1989, West et al. 1997). Allometric equations for trees are typically created by measuring stem diameter as well as height and wood specific gravity (ρ) (although the latter two are less common) for a small number of trees, which are then felled and weighed. Once the masses of the felled trees are estimated, a statistical regression is created to relate tree mass to the inventory
data, permitting non-destructive estimation from that point forward. Biomass density (Mg ha\(^{-1}\)) is then calculated at the stand-level by applying an allometric regression to a much larger inventory, summing the resulting masses, and dividing by the area.

Error is introduced and propagated at each step in creating and applying allometry. Here we define error as statistical uncertainty, distinct from a methodological mistake. Over the past century a variety of allometric equations have been developed for hundreds of tree species (e.g., Feldpausch et al. 2010), and in some cases a generic equation has been developed for entire regions, such as in tropical forests (Chave et al. 2005) and North American forests (Jenkins et al. 2003). Yet the question of how error in estimates of biomass density propagates from the tree to landscape to regional scales has only begun to be rigorously addressed (Ketterings et al. 2001, Chave et al. 2004). Furthermore, the majority of tree allometries have been developed for forest ecosystems, with only a handful of studies from African savanna ecosystems (Rutherford 1979, Nickless et al. 2011).

Tree-level errors of allometry will average out, to some degree, at the stand level with sufficiently large plot size assuming unbiased measurement of diameter and height. However, further uncertainty is introduced by the selection of an allometric model, such as between a species-specific or generic allometry. For example, it is often the case an equation specific to a particular species of interest may be available but was constructed from a small sample size, with diameter as the only predictor of mass, or from trees smaller than those to be predicted. In contrast, generic models based on hundreds of trees can afford to include multiple predictor variables (e.g. diameter, height, \(\rho\)) but span a variety of species, geographic regions, and/or environmental conditions not
representative of the survey site. An allometric model can only reliably predict biomass within the range of the largest trunk diameters and heights of the originally harvested trees; applying an allometric equation to trees larger than those used to create the allometry can result in large systematic errors that do not average out with increasing sample size (Chave et al. 2004).

At landscape scales a second type of sampling error arises, dependent upon how well plots represent spatial variation in the distribution of stand structure and composition, which is in turn a function of environmental gradients (e.g. topography, soil, climate), and disturbance history (Keller et al. 2001). Chave et al. (2004) concluded the cumulative uncertainty in biomass at the landscape scale was 24-30%: 11-22% from choice of allometric model, 2-16% from within-plot sampling error (i.e. varies with plot size), 10% from landscape-scale sampling error (i.e. between plot variance), and a small fraction from measurement error. This study and many others have emphasized allometry as the most important source of error, in part because it does not decrease if plot size or number are increased.

Regional and global estimates of biomass face even more challenges than those at the landscape scale, yet these large scales are of ever increasing relevance to observing changes in fuelwood availability over large rural regions, and to monitoring aboveground carbon pools of entire countries. Large-area biomass monitoring is now considered central for climate mitigation strategies such as REDD+ (Reduced Emissions from Deforestation and Forest Degradation (Gibbs et al. 2007). Airborne and satellite remote sensing capture the variability in environmental factors necessary to scale up field biomass estimates to larger spatial and temporal scales (Asner 2009a). Airborne light
detection and ranging (LiDAR) imaging has proven useful for mapping aboveground biomass (AGB) over areas up to millions of hectares, by measuring vegetation height at high resolution (e.g. <1 m), which is then correlated to field-measured biomass (Asner et al. 2010, Asner et al. 2012c). As a result of these developments with airborne LiDAR, increasing importance has been placed on the uncertainty of individual biomass samples derived from the data (i.e. pixels typically 0.1 – 0.25 ha). The fact that uncertainty from field estimates, particularly allometry, is propagated into airborne AGB estimates has been used to argue that airborne estimates are inherently less accurate than field estimates. While LiDAR is currently the most effective method for estimating landscape-scale biomass and provides the large sample sizes necessary to relate biomass to the multiple environmental factors encountered at regional scales, there remains a need to quantify and minimize uncertainties in LiDAR estimates at the plot scale. This would both increase the accuracy of ecosystem-scale biomass maps derived directly from airborne LiDAR data and improve regional and global biomass models calibrated on LiDAR AGB estimates.

Here we harvested and directly weighed all woody plant biomass at the plot-scale, immediately after collecting airborne LiDAR data, to: a) determine the degree to which allometric error and other field errors affect airborne LiDAR AGB estimates; and b) quantify and reduce the error resulting from plot-level averaging of canopy height by developing and testing a new object-based AGB prediction method capable of performing crown segmentation and extracting maximum height (rather than the mean) and crown area for each tree. We conducted the study in an African savanna, as these ecosystems have rarely been studied with regard to aboveground biomass and have
limited allometry, yet provide a majority of fuelwood for Africa’s energy supply (Brouwer and Falcão 2004, Madubansi and Shackleton 2007), and play a significant role in the global carbon cycle (Asner and Archer 2010).

**Methods**

*Overview and definitions*

Here we provide a brief summary on how a biomass harvest and an airborne LiDAR survey were combined to investigate uncertainties in airborne AGB estimates. Thirty field plots were established within the extent of the airborne data, and all stems >5 cm diameter were labeled and measured. Since savanna trees commonly have multiple stems, we define “stem” to mean all aboveground woody components, including trunk and branches, that can be traced to a single point of emanation from the ground. “Tree” in turn refers to one or more stems emanating from a central rootstock; in cases where this was ambiguous, stems of the same species with mostly overlapping crowns were delineated as a tree. All woody stems within each plot were then destructively harvested and weighed (details below). These stem AGB measurements were summed to the tree and plot level to calibrate and validate three models: (i) a field-only allometric equation (stem level), (ii) an existing airborne LiDAR model (plot level), (iii) a new airborne LiDAR object-based model (tree level). Finally, variants of the airborne models were calibrated using allometry-estimated mass in place of harvested mass to directly measure the propagation of allometric error into airborne AGB estimates.

For model comparisons, we define “relative error” of each stem as the deviation of the predicted AGB from the measured AGB, relative to measured AGB:
relative error = 100 \times \frac{\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{harvested}}}{\text{AGB}_{\text{harvested}}} \quad \text{Eq. 1}

Error in AGB typically increases with AGB rather than remaining constant, thus we find it more relevant to express residual error as a percentage of AGB rather than in units of mass or log(mass) (as often reported for RSE). Thus we use the standard error of the normalized residuals (RSE$_{rel}$) as a measure of predictive power:

$$RSE_{rel} = \sqrt{\frac{\sum (\frac{\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{harvested}}}{\text{AGB}_{\text{harvested}}})^2}{n-2}} \quad \text{Eq. 2}$$

The standard error of the residuals (RSE) was also computed as a measure of absolute error:

$$RSE = \sqrt{\frac{\sum (\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{harvested}})^2}{n-2}} \quad \text{Eq. 3}$$

Biomass predicted using a log model were first back-transformed and multiplied by the Baskerville et al. (1972) correction factor $CF = e^{\left(\frac{\sigma^2_{\log}}{2}\right)}$ (where $\sigma_{\log}$ is the regression RSE in log units). CF corrects for an under-prediction of AGB caused by an assumption of the least-squares regression that the response variable (mass) is normally distributed, when in fact it is log-normally distributed (Beauchamp and Olson 1973). All statistics, including RSE, $R^2$, AIC, were computed on these back-transformed and corrected values in the statistical software R. Bias (%) was defined as the mean of the relative errors.

**Study Site**

The study site was located 12 km north of Phalaborwa, South Africa and 5 km west of Kruger National Park (KNP) on the Pompey property (-23.830880°S, 28.918860°E).
31.101345°E) owned by Palabora Mining Company (PMC, Fig. 7). The site was selected because: (i) the composition of the woody vegetation is representative of a much larger region, including most of the northern half of KNP and neighboring parts of South Africa, Zimbabwe, and Mozambique (ii) the vegetation was soon to be cleared for a strip-mining operation. The site is characterized by hot, wet summers (diurnal temperate range of 20 - 47°C) and dry, cool winters (11 – 25°C), with a mean annual precipitation of 481 mm yr⁻¹ (South African Weather Service data for Phalaborwa, 1960 to 2011). Low-intensity grass fires occur infrequently (several per decade). Mammalian browsers typical of the region (giraffe, eland, kudu and impala) populate the site but were not abundant.

The dominant woody plant species were *Colophospermum mopane* (Fabaceae), *Combretum apiculatum* (Combretaceae), and *Dalbergia melanoxylon* (Fabaceae), depending on location, with 15 additional woody species harvested: *Acacia exuvialis* (Fabaceae), *Albizia harveyi* (Fabaceae), *Acacia nigrescens* (Fabaceae), *Combretum imberbe* (Combretaceae), *Commiphora africana* (Burseraceae), *Commiphora glandulosa* (Burseraceae), *Commiphora mollis* (Burseraceae), *Dichrostachys cinerea* (Fabaceae), *Grewia bicolor* (Malvaceae), *Grewia monticola* (Malvaceae), *Lannea schweinfurthii* (Anacardiaceae), *Philenoptera violacea* (Fabaceae), *Sclerocarya birrea* (Anacardiaceae), *Terminalia sericea* (Combretaceae).

**Airborne data collection**

The Carnegie Airborne Observatory (CAO) collected discrete-return LiDAR data over the site in April 2010 (Fig. 7). A pulse repetition frequency of 50 kHz was used to generate three-dimensional maps of tree canopy structure at 0.56 m laser spot spacing
(aircraft altitude = 1,000 m). Flights were planned with 100% repeat coverage, and therefore LiDAR point density averaged two points per 0.56 m spot. LiDAR spatial errors were less than 0.20 m vertically and 0.36 m horizontally (Asner et al. 2007, Asner et al. 2009). A woody canopy height map was computed by subtracting a ground DEM (classified from LiDAR last return elevation) from a canopy surface DEM (first return elevation). A physical model was used to estimate both DEMs using the Terrascan/Terramatch (Terrasolid Ltd., Jyväskylä, Finland) software package. The vegetation height map served as the primary input to the airborne AGB estimation methods. A low minimum height threshold (0.2 m) was used to avoid removing too much of the shrub layer used by the object-based method. This threshold was also found to offer a minor improvement for the plot-averaging LiDAR method, compared to the previously used threshold of 1.5 m (Colgan et al. 2012a).

Field inventory of structural attributes

Prior to harvest, thirty plots of 30 m diameter (0.071 ha) were established with the center location of each plot recorded using a differentially corrected Global Positioning System (GPS) receiver (GS50 Leica Geosystems Inc.). Each stem >5 cm in basal diameter (and a sample of stems 2 - 5 cm) within each plot was given an ID number, measured for stem diameter D and height H, and identified to species. Stem diameter was measured as basal diameter 10 cm above ground instead of diameter at breast height due to the ubiquity of multi-stemmed trees. Elliptical crown area was measured at the tree level using two perpendicular crown diameter measurements taken with a transect tape (multi-stemmed trees had a single crown area measurement). The GPS location of each tree was also recorded using the Leica GPS receiver, although crown outlines traced onto
LiDAR data maps proved more useful for tree-level registration, particularly for small crowns.

*Harvesting and weighing biomass*

All woody stems within each plot were destructively harvested and weighed between May and July, 2012 (n = 3,068 stems weighed independently, although many more with D < 5cm were cut and weighed in bulk). Two types of harvest methods were used to develop highly accurate allometry and 30 plot measurements of biomass, where each plot had 100+ stems on average. Harvest-method “A” stems had leaves picked and then the entire wood wet (“green”) mass was weighed on a hanging scale (0.1 kg precision, 200 kg capacity); often this required chain-sawing the stem into 0.5 m wide pieces that could be lifted onto the scale. For large stems (D > 10 cm), it was often impractical to pick off every leaf. Instead, the smallest twigs with leaves were cut from the other branches, twigs and leaves were weighed mixed in bulk, one or more subsamples of the bulk pile (~10-20% of bulk mass) were defoliated, and the subsample twigs and leaves were weighed separately to calculate the twig mass fraction for that tree. Type “A” stems also had their water content (WC) measured by cutting a horizontal cross-section from the base of each stem (hereafter referred to as a “disc”), which was weighed in the field with a mass balance (0.005 g precision for discs <150 g or 1 g precision for discs >150 g). Discs were oven-dried at 100°C until the mass equilibrated, and then re-weighed. WC was computed as the difference in mass before and after drying, divided by wet mass. Final stem dry mass was computed as the wood wet mass (trunk, branches, disc) multiplied by (1 – WC). To account for variation in WC within larger trees (stem D > 10 cm), the branches were partitioned into size classes (<2 cm, 2-7
cm, 7-20 cm, 20-40 cm, and >40 cm branch diameter), weighed separately, and sampled for water content.

For harvest-method “B”, stems still had their entire wet mass weighed in the field, but without leaf separation or water content sampling. Stems were harvested in this way to expedite the weighing process, to ensure a sufficient number of plots could be cleared to validate airborne estimates of plot-scale AGB. After collecting over 100 “A” stems for each of the three dominant species (C.mop, C.api, D.mel), the remaining stems for these species were collected using method “B” (large trees and all other species were type “A”). Equations estimating wood mass fraction ($WF_{est}$) and water content ($WC_{est}$) as functions of stem diameter were created from the type “A” stems for the three species harvested using method “B”. Also, a visual estimation of leaf flush (LF) was recorded to minimize error for partially or fully defoliated trees (0 = no leaves, 1 = full foliage). The final dry mass for each “B” stem was calculated as the product of wet mass × (1-$WC_{est}$) × ($WF_{est}$ + (1-$WF_{est}$)(1-LF)). We emphasize the allometry only included type “A” mass measurements. Plot totals of harvested AGB included both types, approximately 70% of total AGB used method A and 25% method B; the remaining 5% comprised of AGB where ID labels were lost or in special cases where a tree inside a plot could not be felled (at the request of property owner), and in these cases the contribution to the plot AGB was estimated using the allometry derived from method A stems.

Mean wood specific gravity ($\rho$) for each species was measured as a predictor variable in the new allometry (note $\rho$ was not used to calculate any stem masses). Samples of $\rho$ (n = 88) were computed as oven dry disc mass (100°C) in grams divided by oven dry volume (cm$^3$), which was measured using water volume displaced by each
cookie in a graduated cylinder (1, 2, and 10 cm$^3$ precision cylinders were used to maintain measurement uncertainty <10%). We recognize that green volume is often reported, but green volume could not be measured in the field. However, the high $\rho$ (mean = 0.9) and the low WC (20 – 40%) of most species minimized variation in volume during drying. Dividing the dry wood density by the density of water (1 g cm$^{-3}$) yields the final unitless form of $\rho$. The mean $\rho$ for each species was the predictor variable included in the generic allometric equation.

Field allometry

An allometric model (henceforth referred to as the “Colgan allometry” for clarity) was created from 707 harvested stem masses of 17 species ranging four orders of magnitude in mass (0.2 - 4,531 kg), using linear regression on log-transformed stem D (cm), H (m), $\rho$ (g cm$^{-3}$), and stem mass m (kg):

$$\ln(m) = \beta_0 + \beta_1 \ln(D) + \beta_2 (\ln(D))^2 + \beta_3 \ln(H) + \beta_4 \ln(\rho) \quad \text{Eq. 4}$$

The model form is equivalent to the pan-tropical Model I.1 of Chave (2005) with the exception of an additional second-order term ($\ln^2(d)$). We introduced this term to correct for an empirically observed under-prediction that occurred for all tree species above a certain size class (D > 30 cm, H > 7 m; A.nig, S.bir, C.mop, C.imb, L.sch, Comm). The final back-transformed version of the Colgan generic allometry (Eq. 5, Fig. 8) was calculated by taking the natural exponential of Eq. 4 and then multiplying the right-hand side by the correction factor previously mentioned. For the plot-scale model comparison,
the mass predicted by the allometry for each stem was summed within each plot and divided by plot area to compute stand-level AGB (Mg ha$^{-1}$).

$$m = 0.109D^{(1.39+0.14\ln(D))}H^{0.73}p^{0.80} \quad \text{Eq. 5}$$

A single equation was chosen over species-specific equations since airborne species-detection was not available. Generic equations are also commonly used in field AGB inventories due to limited availability of species-specific equations (especially those built from large diameter trees and large sample sizes). The allometric model by Nickless (2011) for broad-leafed South African trees was selected for comparison to the Colgan allometry and airborne methods as it is as the best external allometry currently available for trees in the region and has been used in previous studies (Colgan et al. 2012a). The Nickless allometry used only stem diameter as a predictor variable and is included in Table 1. We applied the Nickless allometry in the same manner as the new allometry to predict plot-level mass, although care was taken to not apply the Nickless allometry to stems above the largest diameter used to construct it (33 cm). For trees above this diameter we instead applied a generic allometric equation for temperate trees (including hard maple, oak, hickory, beech species) with sufficiently large maximum diameter (230 cm) from Jenkins (2003). The Jenkins allometry also only uses stem diameter.

*Plot-averaged LiDAR biomass estimation*
To address how allometric error affects AGB estimates from current airborne LiDAR methods, we utilized a LiDAR regression model used in a previous KNP biomass survey (Colgan et al. 2012a), henceforth referred to as the “plot-averaged” (PA) model. This model uses a single predictor variable derived from LiDAR data, H×CC, where H is the mean top-of-canopy height of a plot and CC is the canopy cover of a plot. Both H and CC were extracted from a LiDAR vegetation top-of-canopy height map: H is computed as the mean of pixel height values >0 m within each 30 m diameter plot circle, and CC is computed as the fraction of pixels >0 m in height. The response variable of the PA method is plot-scale AGB, which is typically estimated by applying allometry to field inventory. Here we first trained the model using harvested plot AGB; this first version we refer to as “PA harvest”. We then estimated the AGB of the same 30 plots using the Colgan and Nickless allometries and used these as training input for two additional versions of the PA LiDAR model, “PA Colgan” and “PA Nickless”. During model calibration all three versions of the PA model used the same H×CC dataset; only the response variable, AGB, was varied. Unlike the allometry and object-based methods, the PA model required plot-level AGB rather than tree-level AGB for model calibration, limiting the maximum sample size to 30 plots. Therefore, k-fold cross-validation (k = 3, # runs = 1,000) was used for the PA method instead of dedicated validation plots. The final PA model coefficients listed in Table 1 used all 30 plots for calibration.

Object-based LiDAR biomass estimation

An object-based (OB) model was developed to predict AGB at the tree level using airborne LiDAR data (Fig. 9). The model consisted of four parts: 1) segmentation of
LiDAR vegetation height map into tree crown objects 2) extraction of maximum height (m) and projected area (m$^2$) for each crown object 3) prediction of AGB (kg) for each crown 4) summation of crown-level AGB within each plot to estimate plot-level AGB (Mg ha$^{-1}$).

Crown segmentation was performed using the eCognition (Definiens Developer 8.7) software package, with the following customized “region growing” algorithm and two LiDAR inputs: a vegetation top-of-canopy height map and a return intensity map. The algorithm was iteratively developed until the automatically generated object outlines matched ground-verified crown outlines visually delineated in the field (n = 124 trees amongst seven plots) and traced onto the LiDAR vegetation height map (solid colors in Fig. 9d). The seven plots were selected non-randomly to cover the full range of size classes and dominant species.

In the first step, a pixel was classified as a “crown seed” (Fig. 9b) if all three of the following conditions were met: 1) its height >0.5 m 2) the surrounding pixels were of similar height 3) the surrounding pixels were of similar LiDAR return intensity. The second and third criteria were satisfied if the “coefficient of variation” (CV) of neighboring height and intensity were each below given thresholds (0.3 and 0.45, respectively), where CV was computed for each pixel as the standard deviation of the height (or intensity) of the eight neighboring pixels, divided by the height (or intensity) of the center pixel. The second criterion was the most important factor because it was a measure of flatness; the third criterion was later added as an incremental improvement in cases where two crowns were the same height but had different LiDAR reflectance.
properties (e.g. different leaf chemistry, leaf area index). A pixel was classified as an “edge” if h > 0.5 m but did not satisfy the height CV and intensity CV criteria. The next steps were to merge all neighboring seed pixels into crown objects, grow each crown object by one pixel but only into edge pixels (to prevent merging of trees), and split oblong crowns with roundness > 0.6 (Fig. 9c). The final crown objects were labeled as “tree crowns” if their maximum $H_{obj}$ was >1.5 m or otherwise as “shrubs”. This crown segmentation algorithm was then applied to the entire LiDAR height map (1537x1256, Fig. 7), producing over 23,000 tree objects in under a minute on a PC workstation (Intel Xeon 3.1 GHz, 6 GB memory). The projected crown area ($m^2$) and maximum height (m) were calculated for each tree object using eCognition Developer 8.7 (Trimble Germany GmbH).

After completing crown segmentation, a regression model was created to relate harvested tree mass (kg) to the automatically generated object area and height:

$$\ln(m) = \beta_0 + \beta_1 \ln(A_{obj}) + \beta_2 \left( \ln(A_{obj}) \right)^2 + \beta_3 \ln(H_{obj})$$

Eq. 6

where $m$ is harvested tree mass (kg), $\beta_i$ are least-squares regression coefficients, $A_{obj}$ is object projected crown area ($m^2$), and $H_{obj}$ is object maximum height (m). The final back-transformed equation used for AGB prediction (Table 1) includes CF in the $\beta_0$ term in the same fashion as for the allometry and includes an $\ln^2(A_{obj})$ term to account for the quadratic relationship observed in the field between crown diameter and height (Fig. S1). The training and validation sets were the same set of 124 trees with crowns visually
registered in the field, but importantly, it was the automatically generated crown area and
height ($A_{\text{obj}}$ and $H_{\text{obj}}$) of each that were correlated to the harvested mass of each tree. The
OB model (Eq. 6) was trained on the harvested AGB of 62 calibration trees, then
accuracy statistics were calculated for a separate set of 61 validation trees (Fig. 10a and Table 1). We refer to this OB model as “OB-harvest”. Two additional OB
models, “OB-Colgan” and “OB-Chave”, were created using the same equation (Eq. 6)
but were calibrated using mass estimated from the Colgan or Chave allometry instead of
harvested mass (Fig. 10b). Note the set of trees used to train OB-Colgan were separate from the tree used
to create the Colgan allometry (except for two large trees to maximize the size of tree to
which both models can be applied). A linear regression model to predict shrub AGB was
also created by correlating the crown area of shrub objects, $A_{\text{obj-shrub}}$ ($m^2$), summed over a
plot, to plot totals of harvested AGB (kg) of stems < 5cm diameter (“small stem AGB”):

$$m_{\text{plot-shrubs}} = 3.04 \sum A_{\text{shrub-obj}} - 111.0 \quad \text{Eq. 7}$$

Finally, the object-level AGB predictions were converted to stand-level AGB by
summing all object masses (tree and shrub) within each plot and dividing by plot area,
using the center point of each object to determine if it was inside or outside the plot.
Stand-level statistics (e.g. RSE_{rel}) for the object-based model were computed on a
validation set of plots that did not contain the trees used in model calibration: $n = 23$
validation plots for OB-harvest and n = 10 validation plots for OB-Colgan (since both allometry and object-based calibration plots were excluded).

Results

Harvested biomass

Total harvested, wood dry mass was 57,239 kg from more than 3,000 stems; mean harvested AGB averaged over all 30 plots (2.12 ha total) was 27.0 Mg ha\(^{-1}\), with the lowest plot AGB at 11.9 Mg ha\(^{-1}\) (consisting of \textit{C.mop} shrubland with over 6,000 stems/ha) and maximum plot AGB at 92.3 Mg ha\(^{-1}\) (which contained only 410 stems/ha but included large \textit{A.nig} and \textit{C.imb} trees). The harvested size classes ranged from \(D = 2 - 79.3\) cm, \(H = 0.5 - 15.5\) m, with the largest tree having a dry mass of 4,531 kg (\textit{A.nig}). Stems less than 5 cm diameter accounted for 8\% (median) of plot-level harvested AGB, although two plots containing \textit{C. mop} shrubland (~2 m tall) had 84\% harvested AGB from stems < 5cm. Mean \(\rho\) was 0.90 ± 0.02 (\(n = 88\)) and varied widely between species from 0.55 for \textit{S. bir} to 1.20 for \textit{C.imb}, consistent with previous studies inside KNP and elsewhere in South Africa (Van Wyk and Van Wyk 1997). As expected water content (WC) was inversely related to \(\rho\), with mean WC = 30 ± 0.4\% (\(n = 749\)) ranging from 11\% for \textit{D.mel} to 75\% for \textit{C.mol}. After calculating a weighted-mean WC for each tree, whereby we used the mass of each branch size class to weight branch WC, we found tree WC did not vary significantly with trunk diameter (\(p < 0.05\)) except for \textit{C.mop} and \textit{T.ser}. As a result, linear models relating WC to diameter for \textit{C.mop} and \textit{T.ser} were used to calculate dry mass, whereas mean WC was used for all other species.
Tree-level uncertainties in airborne biomass estimation

Predictions of biomass at the tree level using the object-based model revealed similar accuracy to that of the traditional approach of applying allometry to field-measured stem diameter and height measurements, without any use of airborne data (Table 1). When using the harvested mass to train the object-based approach, we found the tree-level error of the object-based method (RSE_{rel} = 63%) to be very similar to that of the Colgan allometry (RSE_{rel} = 64%). This object-based error was low, relative to the field allometry, despite the larger sample size used to train the allometry (n = 707) relative to the object-based model (n= 62), the object-based approach measures crown area rather than basal area, and that the object-based approach does not have any knowledge of species (whereas the Colgan allometry requires the species-mean wood density). Although object height or crown diameter alone were inferior predictors of stem mass (RSE_{rel} = 90% and 108%, respectively; see Fig. S2), we found using a compound variable of both crown area and H substantially reduced the uncertainty at the tree-level (RSE_{rel} = 63%). It should be noted the lack of species detection may have had a diminished effect because the object-based model was validated at the tree-level primarily on the three dominant species (C.mop, C.api, A.nig); nonetheless, the observed variance in ρ remained moderately high between these species (ρ = 0.75 – 1.2, 95% CI), suggesting species detection could provide further improvement.

We then tested whether destructively-harvested mass sufficiently improves airborne predictions to justify creation of a separate set of “airborne allometry”. We compared the error of the model, calibrated using harvested mass (
Fig. 10a), to the error of a model with the same predictor variables (H, Acr) but calibrated with allometry-estimated mass (Fig. 10b). There was a small increase in the standard error (RSE\textsubscript{rel} = 63% vs. 68%) and no difference in the variance explained (R\textsuperscript{2} = 0.87 for both), indicating that training the object-based method directly on harvested biomass afforded little benefit and that training on allometry-estimated mass can produce a nearly equivalent model.

In the same way that traditional field measurement errors of individual tree biomass mostly average out at the plot scale with unbiased measurements (Chave et al. 2004), we found much of the uncertainty in the object-based airborne method averaged out at the plot scale. The prediction error (RSE\textsubscript{rel}) of the object-based estimate dropped from 68% of an individual tree’s true (harvested) mass to 14% of plot mass, and this includes allometric error introduced during training of the object-based model on biomass estimated from the Colgan allometry.

**Discussion**

*Comparison of field-only allometry accuracies at the plot scale*

In order to interpret how allometric error and other field-based uncertainties propagate into airborne biomass estimates, we first compared the plot-scale prediction accuracies between three allometric models (Nickless (2011), Chave (2005), Colgan (this study)), using only field measurements to estimate biomass and using harvested AGB of validation plots as “truth” (
Fig. 11). The higher residual error and bias of the Nickless allometry (56% and 43% of harvested AGB, respectively) relative to the Colgan allometry ($RSE_{rel} = 16\%$, bias = 4%) were likely due to a limited number of large trees used to construct the Nickless allometry ($D < 33$ cm) and the use of $D$ as the only predictor variable, which does not account for the large inter-specific variation in $\rho$ nor variation in $D:H$ ratios. Although it could be argued the Colgan allometry should clearly be more accurate because it is from the same site as the validation plots, we emphasize the predictive error for the Colgan allometry is based on validation plots not used in the construction of the allometry, and that the collection of species used by Nickless (2011) was nearly identical to this study.

Biomass estimates from a third allometric model were also compared due to recent interest in the extent to which the pan-tropical allometry of Chave et al. (2005) is applicable to Africa, primarily due to its successful application elsewhere in the tropics and large sample size (Feldpausch et al. 2010, Vieilledent et al. 2011, Asner et al. 2012a). Yet few African trees were included in the model calibration, the allometry was created in tropical forests (no savannas), and there is a paucity of biomass harvests on the African continent available for validation. Nonetheless, the Chave I generic model, which includes $\rho$, $D$, and $H$ but was calibrated for dry tropical forests, more accurately predicted our harvested plot AGB than the Nickless allometry, across all statistical metrics ($RSE_{rel}$, AICc, bias, $R^2$; see Table 1), and far outperformed the Chave II model which excludes $H$ ($RSE_{rel} = 43\%$ vs. 229%). As expected, the Chave I equation was increasingly accurate for the larger trees in our harvest dataset but greatly over-predicted biomass for small trees, but overall Chave I had substantially higher residual error and bias than the Colgan allometry (Table 1).
Contribution of allometric error to uncertainty in airborne estimates of biomass

While the application of allometry is necessary to non-destructively estimate tree biomass, it is unknown to what extent allometric error contributes to the total error in airborne biomass predictions. Beginning with the more established of the two airborne LiDAR methods, comparison between the three plot-averaging (PA) LiDAR models (Fig. 5 and Table 1) revealed allometric error accounted for one-third to one-fifth of total airborne error, depending on whether the Nickless or Colgan allometry was used, respectively. Calibration of the PA model on the mass estimated by the Nickless allometry, as done previously in Colgan (2012a), resulted in a high bias (50% over-prediction) and residual error of 50% across all biomass densities. Yet when trained on harvested biomass (i.e. zero allometric error), the PA model still yielded a residual error of 35% but effectively no bias (1%). This demonstrates how systematic error (bias) in the allometry, rather than heteroscedastic random error, had the largest influence on PA airborne estimates and does not average out at larger scales.

The same trend was observed in the object-based (OB) model, where allometry contributed little additional error if it had low bias to begin with. Importantly, we found training the object-based model on mass estimated by the Colgan allometry, in place of harvested mass, only increased the plot-scale residual error from 17% to 22%. The OB model trained on the Colgan allometry initially had a lower residual error (14%) than the field-only approach using the Colgan allometry (16%), which is likely due to the lower number of validation plots resulting from excluding field plots used in both the allometry and object-based model calibrations (n = 18). Alternatively, using all 30 harvested plots as the validation set actually increased the residual error to 22%, which we use as a more
conservative error estimate for the OB-Colgan model. Even after taking this into account, allometric error still accounted for less than one-quarter of the total plot-scale uncertainty in object-based biomass estimates.

We conclude that airborne LiDAR biomass surveys, where destructive harvesting is rarely an option, can be calibrated on biomass estimated from field allometry with approximately a 30% increase in total uncertainty (compared to harvesting and weighing trees within overflight areas) and with little to no additional bias. Furthermore, our object-based LiDAR model, even trained on allometry-estimated mass, was more accurate than the conventional, plot-averaging LiDAR model trained on harvested mass. This assumes the allometry has a low prediction bias and is applied only within the size classes used to construct it; violation of either assumption can quickly lead to biases that propagate into airborne estimates that do not average out at the landscape scale. We stress even a small number of individually harvested and weighed trees (e.g. n = 40) can provide critical validation of low bias when allometry is applied to a new study site.

Reducing non-allometric error in airborne biomass estimates

The majority (~75%) of the residual error in airborne biomass estimates came from sources other than allometry, which we interpret here by comparing the plot-averaging LiDAR and object-based LiDAR models trained on harvested biomass. The observed difference in predictive accuracy between these two models was primarily dependent on how well each approximated the underlying ecological and physical relationships between height, canopy area, and mass (i.e. choice of “airborne allometric model” but we avoid this term for clarity). From the large body of literature on field
allometry, the most accurate and parsimonious biomass allometries estimate wood volume in some fashion and then multiply by wood density (Schenck 1905, Gray 1956, Cannell 1984). In the case of airborne LiDAR, the same is true: the ideal metric is proportional to wood volume (if not mass), but neither stem D nor \( \rho \) is directly measurable from the air. Height is easily and accurately measured from the air. Crown area can also be measured from the air but is often overlooked in tropical forests and plantations, where measurement of the crown area of individual trees is difficult due to overlapping canopies, or is irrelevant where there is a homogenous canopy surface (Asner et al. 2002, Palace et al. 2008). Where tree crown area is measurable, such as in savannas, allometric theory states that crown area should be roughly proportional to stem basal area, and thus the volume term \( H \times A_{cr} \) should be similarly proportional to wood volume.

The plot-averaging LiDAR approach used a predictor variable (\( H_{\text{plot}} \times CC \)) based on this concept but for plots rather than individual trees: \( H_{\text{plot}} \) is the mean of all heights within a plot and CC is plot canopy cover (a proxy for total crown area). The advantages of the plot-averaging method are its simplicity and ability to adapt to the large variability in CC common in savannas. However, no distinction is made between individual trees, and, importantly, multiple trees contribute multiple samples of canopy height, all of which are horizontally averaged into the single height metric, \( H_{\text{plot}} \). This implies that \( H_{\text{plot}} \) and CC are linearly interchangeable. Yet the underlying nonlinear relationships between height, crown area, and mass of an individual tree can lead to large prediction errors, particularly in savannas where structural heterogeneity is large. For example, consider two hypothetical but realistic plots, one with shrubs \( H_{\text{plot}} = 2 \) m and CC = 75%, and the
other containing a single tree with $H_{\text{plot}} = 10$ m but covering only 15% of the plot area. The plot-averaging model will predict the same AGB even though the second plot contains substantially more AGB (e.g. by a factor of 2-5).

The object-based method presented here avoids these issues by calculating a separate volume metric, $H \times A_{cr}$, for each tree crown. A constant $\rho$ is implied but this is also true of the plot-averaging method. A critical aspect of the object-based method is that a single, maximum height can be extracted per crown, reducing the dilution effect that occurs when averaging many height samples from a given tree. Another possible reason for the higher accuracy of the object-based method is less “intrusion” error (and exclusion). We define this for the plot-averaging method as a tree outside a plot whose canopy intrudes into the plot, thereby artificially increasing $H_{\text{plot}}$ (and vice versa). For the object-based method, a similar error is created when, for example, the center of a tree crown lies inside a plot, even though the stem base lies outside the plot. Although these errors may appear similar, every intruding and escaping branch affects the plot-averaging method, whereas the object-based method is affected only in the rare case of a stem located on the plot boundary but far from its canopy center. Additional work is required to quantify intrusion error, although it will have a diminishing influence in larger plots.

Conclusions

While the mass of an individual tree is still slightly better estimated in the field than from the air, the mass of a forest or savanna is best estimated with a combination of remote sensing and field observations. While one of the strengths of airborne LiDAR biomass estimation rests in mapping large, contiguous areas to reduce ecosystem-scale
sampling error, the object-based method tested here demonstrates that airborne LiDAR can produce plot-level estimates that are as accurate as traditional field allometry and roughly double the accuracy of existing LiDAR biomass estimation methods. Object-based methods are particularly well-suited to open-canopy systems, such as savannas, where the ability to extract the maximum height of individual trees substantially reduces uncertainty, rather than a mean canopy height of tens or hundreds of trees. Harvests at the plot-scale provide a much needed standard against which non-destructive techniques can be compared, and when done in careful collaboration with mining or other extractive industries, can utilize areas prior to clearing. The advances reported here are immediately applicable to conservation, resource management and policy development efforts requiring ever improving biomass mapping approaches.

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Table 1. Comparison of predicted AGB to harvested AGB for a variety of field and airborne methods at stem, tree, and plot (0.07 ha) scales. Model calibration statistics (top half) for external allometry (Nickless, Chave) are from the original source, whereas calibration statistics for Colgan allometry calibration statistics are from this study. Validation statistics (bottom half) for all models were calculated using harvested validation datasets from this study (which were separate from the calibration datasets, unless otherwise noted).

<table>
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<th>Model calibration Type</th>
<th>n_cal</th>
<th>R²_cal</th>
<th>β₀</th>
<th>β₁</th>
<th>β₂</th>
<th>β₃</th>
<th>β₄</th>
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<td>0.144</td>
<td>0.729</td>
<td>0.805</td>
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<td>-</td>
<td>-</td>
<td>-</td>
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<td>0.97</td>
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<td>0.252</td>
<td>1.73</td>
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<tr>
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<tr>
<td>OB harvest</td>
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<td>61</td>
<td>0.87</td>
<td>97.8 kg</td>
<td>22%</td>
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<td>61</td>
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<td>61</td>
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<tr>
<td>Colgan allm. (sum)</td>
<td>16%</td>
<td>12</td>
<td>0.98</td>
<td>3.7 Mg/ha</td>
<td>-4%</td>
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<tr>
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<td>30</td>
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<td>45%</td>
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<td>0.63</td>
<td>10.0</td>
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<td>-3%</td>
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<tr>
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<td>50%</td>
<td>10×3</td>
<td>0.32</td>
<td>7.9</td>
<td>50%</td>
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</table>
Notes: OB = object-based airborne LiDAR method, PA = plot-averaged airborne LiDAR method. Type is the measurement type (F = field allometry applied to field inventory, A = airborne LiDAR trained on harvested biomass, A+F = airborne LiDAR trained on allometry-estimated biomass), n = sample size (cal = calibration set, val = validation set), $R^2$ is the adjusted coefficient of determination (adjusted for # parameters), $\beta_x$ are linear model coefficients ($\beta_0$ includes CF, see text), Eq. is equation form (see below), RSE$_{rel}$ is the standard error of the estimate relative to plot AGB (see text), RSE = Residual Standard Error (in kg for stem and tree scale, Mg ha$^{-1}$ for plot scale), Bias = mean signed relative difference = mean((AGB$_{pred}$-AGB$_{har}$)/AGB$_{har}$), AICc the Akaike Information Criterion corrected for small sample size.

† Plot-averaged (PA) RSE$_{rel}$, $R^2_{val}$, and RSE were computed using k-fold cross-validation (k=3, nruns = 1000) since the number of plots was limited to n = 30 for PA model calibration. Bias was computed once for all 30 plots in the same manner as for the other methods.

Equation forms (Eq.) are:

A) \[ AGB = \exp[\beta_0 + \beta_1 \ln(D) + \beta_2 (\ln(D))^2 + \beta_3 \ln(H) + \beta_4 \ln(\rho)] \]
B) \[ AGB = \exp[\beta_0 + \beta_1 \ln(D)] \]
C) \[ AGB = \exp[\beta_0 + \beta_1 \ln(\rho D^2 H)] \]
D) \[ AGB = \exp[\beta_0 + \beta_1 \ln(D) + \beta_2 (\ln(D))^2 + \beta_3 (\ln(D))^3 + \ln(\rho)] \]
E) \[ AGB = 10^{\beta_0 + \beta_1 \log_{10}(A_{obj}) + \beta_2 (\log_{10}(A_{obj}))^2 + \beta_3 (\log_{10}(A_{obj}))^3} \]
F) \[ AGB_{plot} = \beta_0 + \beta_1 H_{plot} \cdot CC_{plot} \]

where AGB is dry aboveground stem biomass (kg), $\beta_x$ are linear model coefficients ($\beta_0$ includes CF, see text), D is basal stem diameter (cm), H is stem height (m), $\rho$ is wood specific gravity (unitless), $A_{obj}$ is tree object crown area (m$^2$), $H_{obj}$ is tree object maximum height (m), AGB$_{plot}$ is plot-total AGB (Mg ha$^{-1}$), $H_{plot}$ is mean canopy height of plot (m), CC$_{plot}$ is fractional canopy cover of plot.
Fig. 7 Map of study site with ‘olo’ indicating vegetation height measured by airborne LiDAR. White circles indicate harvested plots (n = 30), within which all woody vegetation was cut and weighed in the field. The black area to the west represents area already cleared for mining. Note some vegetation shown in red well exceeds 6 m, including the tallest harvested tree (15.5 m, 5.1 tons wet). Inset shows location of study site near Kruger National Park, South Africa. ZW = Zimbabwe, MZ = Mozambique.
Fig. 8 Stem allometry relating field-measured basal stem diameter, D (cm), height H (m), and wood specific gravity ρ (unitless) to destructively harvested stem mass (kg). Each point represents an individual stem. Note D and H were measured for all stems, whereas ρ was measured for a subset of stems and thus a species mean value was used for ρ.
Fig. 9 Creating objects from airborne LiDAR data to measure tree height and crown area for each harvested tree in a given plot: a) initial LiDAR vegetation height map with white circle indicating harvested field plot boundary b) intermediate results of crown segmentation, with yellow pixels representing initial crown “seeds” and purple pixels indicating crown edges c) final object layer, with predicted tree objects in yellow and shrubs in green d) ground truth layer, with solid colors indicating crown areas for individual trees, visually validated in the field prior to harvest (outlines are the predicted objects).
Fig. 10 Comparison of two airborne predictions of tree mass (kg) data using either a) harvested tree mass or b) allometry-predicted mass to train the object-based model (equation in panel). The LiDAR-measured inputs of maximum tree height $H$ (m) and crown area $A$ ($m^2$) were extracted from tree objects automatically identified in the LiDAR data. The same input set of $A$ and $H$ (i.e. same crowns) were used in a and b. The set of trees with crowns visually registered in the field with the LiDAR data ($n = 124$) were split equally into training (squares) and validation (circles) sets. The statistics shown are based only on the validation set. $R^2 =$ coefficient of determination, $RSE_{rel} =$ residual standard error ($\%$), $n =$ number of tree crowns. Comparison of a and b indicates allometric error accounts for only a small increase in uncertainty in the object-based model.
Fig. 11 Comparison of residual RSE$_{rel}$ in plot-level AGB for a variety of field and airborne estimation methods. “Residual error” (RSE$_{rel}$) is expressed in percent of plot-level harvested AGB and is calculated using validation plots only. Plot-averaging airborne RSE$_{rel}$ was based on a 3-fold cross-validation since this model relies on plots rather than trees for calibration.
Fig. 12 a) Bias expressed in percent of stand-level AGB for three non-destructive estimation methods. Spline curves represent point-wise averages of relative error (i.e. mean signed relative difference), where relative error = (predicted AGB – harvest AGB) / harvest AGB. Field allometry alone consistently under-predicted stand biomass for plots with 0-40 Mg ha\(^{-1}\). The bias of the object-based method either matched or outperformed the field allometry throughout most of the range. The canopy-based method significantly underestimated plots <18 Mg ha\(^{-1}\). Note low sample sizes above 45 Mg ha\(^{-1}\) limit extrapolation of the bias curves (only two plots above this level). b) Frequency distribution of the number of harvest plots, representing the proportion of biomass levels across the study site. Near the most frequent biomass levels (14-30 Mg ha\(^{-1}\)), the airborne methods have lower bias than the field allometry.
Appendices

Fig. S1 Relationships between tree height and crown diameter (both field-measured) for the top three most dominant species in terms of biomass. a) Lines are second-order polynomial model fit to individual tree data (b-d), shaded regions represent 95% confidence intervals. The second-order coefficient was statistically significant for *C. apiculatum* and *A. nigrescens* (p<0.05), showing how the ratio of crown diameter to height changes with size for these species. b-d) Points are individual trees, many of which are multi-stemmed (particularly for b and c) where the crown diameter is that of the group of stems and height is the maximum height of the group.
Fig. S2 Prediction of destructively harvested tree mass using a single predictor variable: tree crown area (left column) or height (right column). Top row is field-measured (note crown area is elliptical, derived from two diameter measurements); bottom row are the LiDAR-measured, object-based crown area and max height. SEE is equivalent here to $RSE_{rel}$. Note the LiDAR crown area (c) has slightly lower predictive error than ground-measured crown area, particularly for small crowns, suggesting LiDAR better captures the true crown area that is commonly irregular in small trees. The model under-predicts as height becomes necessary to accurately predict biomass for large trees. Although height alone has stronger predictive performance, including both minimizes predictive error across all size classes, as shown in the final object-based model.
Fig. S3 Stand-level AGB estimated using two airborne-based methods and either harvested AGB or allometry-estimated AGB (see Figure 3) to train the models. Each point represents a harvested field plot. The canopy-based method uses mean, top-of-canopy height and canopy cover to predict plot AGB. The object-based method first estimates tree mass (see Fig. 4) and then sums these within each plot. Comparing a to c and b to d shows allometric error, propagated to the stand-level, is non-negligible but a small proportion of total residual error.
Chapter 4.

Species-specific biomass allometry and form factors of South African trees

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Abstract

Tree biomass is both a fundamental state variable of ecosystems and the critical parameter in effectively monitoring aboveground carbon stocks. Destructively harvesting and weighing biomass is labor intensive, expensive, and prohibited in protected areas. Thus one of the largest sources of error in non-destructively estimating forest biomass is the selection of an allometric model. This is particularly problematic in African savanna woodlands, where limited availability of allometry, small sample sizes, and lack of harvested large trees make it unclear whether species-specific allometries are more accurate than generic models or significantly different from each other. It also remains unclear whether variation in growth form or wood specific gravity ($\rho$) is the principal cause of biomass differences among savanna species. Here we constructed ten species-specific allometric models from 714 destructively harvested stems in savanna woodland near Kruger National Park, South Africa. Three of the four most common woody species had fits significantly different ($p < 0.05$) from one another, with the highest species curve ($Acacia nigrescens$) more than twice the biomass of the lowest ($Sclerocarya birrea$) even for moderately sized trees ($D = 10$ cm). We then compared the form factors (taper) of each species by dividing mass by $\rho$ and cylindrical volume, showing most species are in the range of $F = 0.78-0.80$ without significant variation between most species. These results suggest there are both statistically significant and ecologically substantial differences between the allometries of common savanna species, and that variation in wood density is the primary source of biomass differences between these species.

Key words: destructive harvest, savanna woodland, form factor, Kruger National Park
Introduction

Tree biomass is fundamental both as an ecological state variable and as a tool in effectively monitoring carbon stocks in ecosystems. Biomass is geometrically dependent upon both the volume and wood density of the vegetation, yet the relative importance of each in driving biomass variation at the ecosystem scale is not the same as it is at the level of individual trees. For example, wood specific gravity (ρ) within tropical forests can vary widely between the hundreds of individual tree species per hectare (Baker et al. 2004), yet the biomass at the stand-level is often more sensitive to variation in canopy structure (Asner et al. 2012b). Variation in structure can be expressed as differences in growth form, where trees of equal stem diameters will have different heights and crown diameters depending on their evolved strategies for light competition, nutrient acquisition, and survival under disturbance regimes (e.g. browsing, fire). Recent global studies of diameter-to-height relationships in tropical forests have found significant variation in form factor (Feldpausch et al. 2010), and they stressed the importance of including both height and stem diameter in allometric biomass relationships to capture variation in form factor, as well as including ρ to account for variation in wood density.

A simple allometric model utilizing all three predictor variables ρ (g cm\(^{-3}\)), D (cm), and H (m) to represent a tree’s aboveground mass AGB (kg) as a geometric solid ranging from perfect cone to cylinder, is summarized by Chave (2005):

\[ AGB = F\rho \left(\frac{\pi D^2}{4}\right)H \quad \text{Eq. 1} \]
where F is defined as the tree’s form factor (taper), such that F=0.1 corresponds to a perfect cylinder and F = 0.0333 implies a perfect conical shape. Gray (1956) predicted broadleaf species should have F = 0.06, and Cannell (1984) describes in detail the effect of branch allocation on F.

In contrast to tropical and temperate zones, semi-arid savanna woodlands have low light competition but are water limited (e.g. 400-750 mm yr\(^{-1}\)), and droughts are more common. The resulting open-canopy system leads to tree-grass competition in early life stages, followed by frequent, low-intensity grass fires, and browsing by herbivores. Here we focus on the savanna woodlands in and near Kruger National Park (KNP), South Africa, as a model for measuring and monitoring biomass in savannas. The current best allometry for South African savanna trees is that of Nickless (2011), which assumes a power-law relationship between stem diameter D (cm) and aboveground biomass AGB (kg) of the form:

\[ AGB = \beta_0 D^{\beta_1} \quad \text{Eq. 2} \]

The Nickless allometry provides 17 species-specific equations, covering the dominant woody plant species and many of the secondary species. Dividing the species-specific curves of Nickless by the mean \( \rho \) of each species yields several species-specific wood volume curves that remain distinct from one another. This suggests that variation in form factor between savanna species (e.g. differences in allocation to branch growth for two trees of equal stem diameter) is a considerable driver of differences in tree mass between species, in addition to \( \rho \). If varying \( \rho \) accounted for the majority of the
differences, we would expect the curves to effectively collapse onto one another (within each confidence band), and yet they do not. However, this conclusion rests on the assumption that a power law relationship between D and m is representative of the form factor. Implicit in this assumption is that the ratio D:H is constant with increasing size class, which may hold true for small diameter ranges of the species-specific Nickless allometry. Yet recent field surveys show the size classes of Kruger’s tree populations are well outside the range of the Nickless allometry, particularly Acacia nigrescens and Sclerocarya birrea (Colgan et al. 2012b). Therefore it remains unclear as to what extent form factor accounts for differences in tree mass between savanna woody species, and how this might change for larger trees.

The relative importance of form factor and ρ between species also has implications for airborne estimation and monitoring of aboveground biomass (AGB). Recently airborne LiDAR has been successful used in mapping savanna AGB throughout KNP, and advances in remotely delineating individual trees crown and estimations of their AGB has created the potential for species-specific AGB prediction. Since airborne LiDAR measures 3-D vegetation structure, it can provide information about form factor but does not provide a direct measure of ρ. A second type of airborne sensor, a hyperspectral imager, measures canopy reflectance spectra, which vary with foliar chemical composition and have been used for species mapping near KNP (Cho et al. 2009, Cho et al. 2010, Naidoo et al. 2012). Thus there is now the potential to remotely estimate ρ of individual trees using species prediction from hyperspectral data, yet species prediction introduces a new set of uncertainties which will propagate into AGB estimates. To determine whether species detection will substantially improve airborne
AGB accuracy, we must improve our understanding of the relationship between $\rho$, form factor, and tree mass. It is also equally important to identify which species are both dominant and have significantly different allometric relationships; if two species have nearly identical AGB allometries, then remotely sensed species identification will not improve the predictive accuracy of airborne AGB estimates.

Here we use destructively harvested biomass from a site adjacent to KNP to construct new species-specific allometric equations, which were then used to answer two questions: a) Are the allometrics of common African savanna species sufficiently different from one another to warrant use of species-specific equations over generic allometry? b) To what extent are the differences between species-specific allometries determined by form factor or $\rho$?

**Methods**

**Study Site**

The study site was located 12 km north of Phalaborwa, South Africa and 5 km west of Kruger National Park (KNP) on the Pompey property (-23.830880°S, 31.101345°E) owned by Palabora Mining Company (PMC). The site was selected because: (i) the savanna vegetation is comprised of the same common species found within KNP (*C. mopane* and *C. apiculatum* are dominant woody species), and (ii) the vegetation was slated for clearing by the mining company. The site is characterized by hot, wet summers (20 - 47°C) and dry, cool winters (11 – 25°C), with a mean annual precipitation of about 500 mm yr$^{-1}$. Low-intensity grass fires are frequent, and giraffe, zebra, and other mammalian herbivores populate the site.
The dominant woody plant species at the site were *Colophospermum mopane* (Fabaceae), *Combretum apiculatum* (Combretaceae), and *Dalbergia melanoxylon* (Fabaceae), depending on location, with the following additional species harvested and fit for species-specific allometry: *Acacia nigrescens* (Fabaceae), *Combretum imberbe* (Combretaceae), *Commiphora africana* (Burseraceae), *Commiphora pyracanthoides* (Burseraceae), *Commiphora schimperi* (Burseraceae), *Commiphora mollis* (Burseraceae), *Dichrostachys cinerea* (Fabaceae), *Grewia bicolor* (Malvaceae), *Grewia monticola* (Malvaceae), *Lannea schweinfurthii* (Anacardiaceae), *Philenoptera violacea* (Fabaceae), *Sclerocarya birrea* (Anacardiaceae), *Terminalia sericea* (Combretaceae). Several species were grouped by genus, such as *Commiphora spp.* and *Grewia spp.*, to increase sample sizes after an initial modeling phase showed they had similar allometries. Other species present at the site but not in sufficient number to construct species-specific allometry were *Acacia exuvialis* (Fabaceae) and *Albizia harvey* (Fabaceae).

**Field inventory of structural attributes**

Prior to harvest, thirty plots of 30 m diameter (0.071 ha) were established using stratified random sampling throughout the site, with strata determined by dominant species (*C.api, A.nig/C.mop, C.mop shrubland*) and topography (crest, lowland). Each stem >5 cm in basal diameter D (and a sample of stems 2 - 5 cm) within each plot was given an ID number, measured for D (cm) and height H (m), and identified to species. Stem diameter was measured as basal diameter 10 cm above ground instead of diameter at breast height due to the ubiquity of multi-stemmed trees. Height was measured using a range pole or a laser range finder for large trees.
Harvesting and weighing biomass

All woody stems within each plot were destructively harvested and weighed between May and July, 2012 (n = 3,068 stems weighed independently, although many more with D < 5cm were cut and weighed in bulk). Two types of harvest methods were used to develop highly accurate allometry and 30 plot measurements of biomass, where each plot had 100+ stems on average. Only the first and more accurate type, harvest-method “A”, were used in this study because the sample sizes were already sufficiently high for the three species that had additional stems harvested using method “B”; a concurrent study provides the stand-level harvest results using all harvest types (Colgan 2012, in prep). Harvest-method “A” stems had leaves picked and then the entire wood wet (“green”) mass was weighed on a hanging scale (0.1 kg precision, 200 kg capacity); often this required chain-sawing the stem into 0.5 m wide pieces that could be lifted onto the scale. For large stems (D > 10 cm), it was often impractical to pick off every leaf; instead, the smallest twigs with leaves were cut from the other branches, twigs and leaves were weighed mixed in bulk, one or more subsamples of the bulk pile (~10-20% of bulk mass) were defoliated, and the subsample twigs and leaves were weighed separately to calculate the twig mass fraction for that tree. Stems also had their water content (WC) measured by cutting a horizontal cross-section from the base of each stem, which was weighed in the field with a mass balance (0.005 g precision for cookies <150 g or 1 g precision for cookies >150 g). Wood cross-sections were oven-dried at 100°C until the mass equilibrated, and then re-weighed. WC was computed as the difference in cross-section mass before and after drying, divided by wet mass. Total stem dry mass was computed as the wood wet mass (trunk, branches, cookie) multiplied by (1 − WC). To
account for variation in WC within larger trees (stem D > 10 cm), the branches were partitioned into size classes (<2 cm, 2-7 cm, 7-20 cm, 20-40 cm, and >40 cm branch diameter), weighed separately, and sampled for water content.

Mean ρ for each species was measured for inclusion as a predictor variable in the allometry (note ρ was not used to measure any stem masses). Wood specific gravity was measured from a sub-sample of stems (n = 93) and were computed as oven dry mass (100°C) divided by oven dry volume, which was measured using water volume displaced by each cookie in a graduated cylinder (1, 2, and 10 cm³ precision cylinders were used to maintain measurement uncertainty <10%). We recognize green volume is often reported but this was not measured in the field; however, the high ρ (mean = 0.9) and the low green WC (20 – 40%) of most species minimized variation in volume during drying. The mean ρ for each species was the final predictor variable included in the generic allometric equation.

Allometry models

To account for intra-specific variation in growth form (D:H ratio), linear regression models of the form shown in Eq. 3 were created to predict stem AGB using both D and H:

\[ AGB = exp(\beta_0 + \beta_1 ln(D^2H)) \]  \hspace{2cm} \text{Eq. 3}

The wood specific gravity was not included since a separate model was fit for each species, making it less necessary. Although including ρ would help account for intra-specific variation, it is typically not measured in non-destructive biomass surveys.
Several general models were also fit, including one of the same form as Eq. 3 (intended only for comparison and not for AGB prediction), as well as a model including ρ (Eq. 4) and a slightly more complex model (Eq. 5) that includes a correction term for larger trees and is the most accurate of the general equations for predicting biomass:

\[
AGB = \exp(\beta_0 + \beta_1 \ln(D^2 H\rho)) \quad \text{Eq. 4}
\]

\[
AGB = \exp(\beta_0 + \beta_1 \ln D + \beta_2 (\ln D)^2 + \beta_3 \ln H + \beta_4 \ln \rho) \quad \text{Eq. 5}
\]

The additional second-order diameter term in Eq. 5 corrects for an under-prediction that occurred for all species above a certain size class (d > 30 cm, h > 7 m) in our dataset. The development and ecological basis for Eq. 5 is discussed more thoroughly in Chapter 3.

For evaluating model performance we define “relative error” of each stem as the deviation of the predicted AGB from the measured AGB, relative to measured AGB:

\[
\text{relative error} = 100 \times \frac{\text{AGB}_{\text{predicted}} - \text{AGB}_{\text{harvested}}}{\text{AGB}_{\text{harvested}}} \quad \text{Eq. 6}
\]

Error in AGB typically increases with AGB rather than remaining constant, thus we find it more relevant to express residual error as a percentage of AGB rather than in units of mass or log(mass) (as often reported for RSE). Thus we use the standard error of the normalized residuals (RSE_{rel}) as a measure of predictive power:

\[
RSE_{rel} = \sqrt{\frac{\sum (\frac{\text{AGB}_{\text{pred}} - \text{AGB}_{\text{harv}}}{\text{AGB}_{\text{harv}}})^2}{n-2}} \quad \text{Eq. 7}
\]

The standard error of the residuals (RSE) was also computed as a measure of absolute error:
\[ RSE = \sqrt{\frac{\sum (\text{AGB}_{\text{pred}} - \text{AGB}_{\text{harel}})^2}{n-2}} \]  \hspace{1cm} \text{Eq. 8}

Values predicted using a log model were first back-transformed, including the Baskerville et al. (1972) correction factor \[ CF = e^{-\frac{\sigma_{\text{log}}^2}{2}} \] (where \( \sigma_{\text{log}} \) is the regression RSE in log units) prior to computing statistics, all of which were performed in the statistical software R.

**Results**

*Species composition of KNP*

The species composition of KNP was determined from field inventories inside the park in 2008 are shown in Fig. 13. We found four species accounted for 77% of the park’s basal area: \( C.mop \) (47%), \( C.api \) (12%), \( S.bir \) (10%), \( A.nig \) (8%). Another 10% is comprised of seven species: \( T.ser \) (4%), \( C.col \) (2%), \( C.imb \) (1%), \( D.mel \) (1%), \( D.cin \) (1%), \( S.afr \) (1%), and \( P.vio \) (1%). The remaining 13% of KNP basal area is composed of 300+ other woody plant species (Van Wyk and Van Wyk 1997). We note that these proportions are based on “upland” areas only, excluding riparian corridors along major rivers. Although riparian zones account for only ~2% of KNP land area, we estimate these areas comprise roughly 10% of Kruger’s total AGB, which would affect the proportions above, especially for riparian species such as \( Diospyros mespiliformis \), \( C.imb \), and \( P.vio \).

*Species-specific biomass allometry*
Simplified relationships using only D (Fig. 14) were created for ten species to compare the effect on predictive power of excluding H. The species included the top five dominant woody species found in KNP and five species with no published allometry. Species-specific allometries to predict mass were fit for the same ten species using a power-law function of $D^2H$ (Fig. 15, Table 1). All had good fits using $\text{RSE}_{\text{rel}}$ and $R^2$ as metrics of predictive performance, with residual errors ranging from 31% and 54% of harvested stem biomass, despite large ranges in AGB (e.g. four orders of magnitude for $A.nig$). Large sample sizes were achieved for $C.mop$ ($n = 371$), $C.api$ ($n = 121$), and $D.mel$ ($n = 102$); species with few stems were only included in the allometry set if they have no published allometry, and in the case of $C.imb$, due to the difficulty in harvesting the extremely high-density wood ($\rho = 1.2$). The final allometry form ($D^2H$) had lower residual error than the D-only allometry for seven out of ten species, with $A.nig$ being the primary exception with substantial under-prediction for the two largest stems. Two general equations were also derived (bottom of Table 1); the first equation is of the same form ($D^2H$) but is intended only for model comparison due to the large range in $\rho$. The second general equation includes $\rho$ in the predictor variable (ala Chave (2005) Model 1) and is intended for application by future users when species-specific allometry is not available; measurement of $\rho$ is not necessary when using this equation to predict AGB because the species-mean $\rho$ listed in Table 1 was used to calibrate the model.

Wood specific gravity and water content

Wood specific gravity was sampled only for modeling purposes (not used in harvest measurement of mass) from $n = 93$ stems, and mean $\rho$ was found to vary widely
between species from 0.55 for *S.bir* to 1.2 for *C.imb* (Table 1). Intra-species variation was relatively narrow with 10%-20% variation, depending on species (Fig. 16a). Water content was sampled for the majority of the stems to calculate dry mass and species mean WC ranged from 21%-60% (Table 1). Relative variation in WC between species was lower than for ρ, with species falling roughly into three major WC classes: seven species with low WC (20-30%), two with medium WC (30-40%), and three species high WC (>40%). As expected water content was found to be strongly correlated to ρ, with 65% of variation in WC explained by a simple analytic model of ρ (Fig. 18) which assumes any tree volume is filled either with cellulose (ρ ≈ 1.5) or water (i.e. maximum moisture content).

**Discussion**

*Significance and relevance of differences between species allometries*

The application of species-specific allometry is more common in temperate than tropical zones, in part due to lower species diversity allowing to be more logistically feasible. However, Chave et al. (2005) and more recently (Vieilledent et al. 2011) have found that a generic model with both large samples sizes and large trees often does more to minimize allometric error in AGB estimates than using species-specific equations, particularly if ρ and H are included as predictor variables. Here we discuss which of the new species’ allometries provide sufficient improvement to warrant their use over a generic model, and whether these species represent a substantial portion of the biomass within KNP.
By comparing the species fits and their associated 95% confidence bands (Fig. 19a – note these are linear models refit using Eq. 1 for later comparison of form factor, but are comparable in form to the allometry in Table 1), it is clear that at least some of the species’ allometry are significantly different from one another (Fig 7a). We found that three of four dominant species in KNP (A.nig, C.mop, and S.bir) can vary in mass by twofold or more for a given stem diameter and height. Interestingly, the second most abundant woody species in KNP, C.api, was not significantly different from A.nig, despite stark differences in canopy morphology and stature. All three genera of Commiphora did not significantly vary from S.bir, whereas L.sch, another less common species phylogenetically similar to S.bir, had allometry quite different from the others. The remaining five species were clustered near the origin or had an insufficient sample size to adequately determine significance. These comparisons suggest that the use of species-specific equations is especially important when predicting the biomass of A.nig, C.mop, and S.bir. However, the general model should be used for stems above the maximum diameter or height for a given species-species equation.

Form factor vs. wood specific gravity in driving biomass

Here we consider conceptual models to better characterize the form factors of each species – the models in this section we consider separate from the prediction models discussed earlier. To model a species’ form factor, we measured the specific gravity per stem to estimate the total cylindrical mass ($\pi/4\rho D^2H$) and found it to be linearly correlated to the actual mass, as expected (Fig. 7b). The resulting slope reflects the form factor $F$ of each species alone. Remarkably, four out of five species (C.api, A.nig, S.bir, and L.sch) had form factors which were not significantly different from one another, with
tapers ranging between $F = 0.078-0.080$ (Fig. 19b). This suggests that wood specific gravity is the principal difference between species-specific allometries. One exception was *C.mop*, which had a taper ($F=0.54$) significantly lower than the remaining four species, and an even lower taper for the largest *C.mop* stems. This suggests *C.mop* has a short and stout form factor, and allocates more growth to lower parts of its canopy with increasing size. One caveat is that the sample size of the $\rho$ measurements for *A.nig* was too low to reliably fit to a model, so the species-mean value for $\rho$ was instead used. It is possible that an increased sample size would change the observed $F$, although we tested the effect of replacing measured $\rho$ with mean $\rho$ for all species and found the same patterns and overlapping confidence bands.

*Implications for biomass estimation and monitoring*

Although a large fraction of the variation between species allometrics is explained by wood specific gravity, it is nonetheless more accurate to use species-specific models which capture both differences in form factor and density as well as other unmodeled variability (e.g. form factors varying with larger tree sizes). The new allometries derived here show wide variation between savanna wooded species. These differences are both statistically significant and large in magnitude, and are thus ecologically relevant. Use of species-specific equations for predicting AGB of the dominant species is recommended, since minimizing residual error in these species will have the greatest impact on stand-level accuracy. Otherwise, the generic equation developed here includes three critical predictor variables ($D$, $H$, $\rho$), has a large sample size and a number of large diameter trees, making the model suitable for predicting the mass for all but the largest of trees found in KNP.
The relationships derived here linking biomass, form factor, and wood specific gravity suggest that variation in wood specific gravity is the primary determinant of biomass variation among savanna species. Rapidly expanding efforts to map biomass by applying general allometries at the stand level, with or without the aid of remote sensing such as radar and LiDAR, may thus need to account for spatially- and taxonomically-explicit variation in species composition in savannas.

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Table 1: Comparison of species allometric relationships, relating stem diameter D (cm) and height H (m) to stem dry mass m (kg):

<table>
<thead>
<tr>
<th>Species name</th>
<th>β₀</th>
<th>β₁</th>
<th>RSEₘₐₓ (%)</th>
<th>RSE (kg)</th>
<th>R²</th>
<th>n</th>
<th>D range (cm)</th>
<th>H range (m)</th>
<th>ρ</th>
<th>WC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A.nigrescens</td>
<td>-2.978</td>
<td>0.989</td>
<td>50%</td>
<td>198</td>
<td>0.97</td>
<td>26</td>
<td>2.1-79.3</td>
<td>1.3-15.5</td>
<td>1.06 ± 0.03</td>
<td>29 ± 2.6</td>
</tr>
<tr>
<td>C.imberbe</td>
<td>-3.528</td>
<td>1.066</td>
<td>31%</td>
<td>83</td>
<td>0.90</td>
<td>9</td>
<td>6.4-38.5</td>
<td>2.5-8.7</td>
<td>1.20 ± 0.09</td>
<td>27 ± 4.0</td>
</tr>
<tr>
<td>C.capriculatum</td>
<td>-2.750</td>
<td>0.941</td>
<td>40%</td>
<td>9</td>
<td>0.88</td>
<td>121</td>
<td>2.3-25.1</td>
<td>1.2-7.9</td>
<td>1.09 ± 0.07</td>
<td>24 ± 0.7</td>
</tr>
<tr>
<td>C.mopane</td>
<td>-2.550</td>
<td>0.895</td>
<td>52%</td>
<td>19</td>
<td>0.92</td>
<td>371</td>
<td>1.2-44.2</td>
<td>0.5-8.8</td>
<td>0.98 ± 0.05</td>
<td>28 ± 0.5</td>
</tr>
<tr>
<td>P.violacea</td>
<td>-2.572</td>
<td>0.91</td>
<td>54%</td>
<td>32</td>
<td>0.87</td>
<td>12</td>
<td>2.2-27.4</td>
<td>0.7-8.6</td>
<td>0.87 ± 0.09</td>
<td>39 ± 1.3</td>
</tr>
<tr>
<td>T.sericea</td>
<td>-3.071</td>
<td>1.007</td>
<td>38%</td>
<td>19</td>
<td>0.71</td>
<td>15</td>
<td>4.5-23.9</td>
<td>1.8-5.6</td>
<td>0.86 ± 0.05</td>
<td>21 ± 1.8</td>
</tr>
<tr>
<td>L.schweinfurthii</td>
<td>-3.576</td>
<td>1.02</td>
<td>34%</td>
<td>12</td>
<td>0.98</td>
<td>37</td>
<td>1.9-40.1</td>
<td>1.4-9.3</td>
<td>0.64 ± 0.06</td>
<td>51 ± 1.0</td>
</tr>
<tr>
<td>Commiphora spp.</td>
<td>-3.538</td>
<td>0.989</td>
<td>46%</td>
<td>8</td>
<td>0.93</td>
<td>73</td>
<td>2.3-29.3</td>
<td>1.0-7.5</td>
<td>0.57 ± 0.20</td>
<td>60 ± 2.6</td>
</tr>
<tr>
<td>S.birrea</td>
<td>-3.982</td>
<td>1.043</td>
<td>42%</td>
<td>56</td>
<td>0.94</td>
<td>16</td>
<td>8.0-57.9</td>
<td>2.0-10.1</td>
<td>0.55 ± 0.06</td>
<td>55 ± 2.0</td>
</tr>
<tr>
<td>D.melanoxylon</td>
<td>-2.092</td>
<td>0.783</td>
<td>54%</td>
<td>1</td>
<td>0.74</td>
<td>102</td>
<td>2.0-10.9</td>
<td>0.5-3.4</td>
<td>0.82 ± 0.06</td>
<td>22 ± 0.8</td>
</tr>
<tr>
<td>All (D²H)</td>
<td>-2.758</td>
<td>0.929</td>
<td>58%</td>
<td>106</td>
<td>0.81</td>
<td>714</td>
<td>1.2-79.3</td>
<td>0.5-15.5</td>
<td>0.90 ± 0.05</td>
<td>33 ± 1.0</td>
</tr>
<tr>
<td>All (D²Hρ)†</td>
<td>-2.708</td>
<td>0.934</td>
<td>50%</td>
<td>85</td>
<td>0.87</td>
<td>714</td>
<td>1.2-79.3</td>
<td>0.5-15.5</td>
<td>0.90 ± 0.05</td>
<td>33 ± 1.0</td>
</tr>
<tr>
<td>All (D²β₁+β₂lnD H β₃ρ β₄) ††</td>
<td>-</td>
<td></td>
<td>52%</td>
<td>37</td>
<td>0.98</td>
<td>707</td>
<td>1.2-79.3</td>
<td>0.5-15.5</td>
<td>0.90 ± 0.05</td>
<td>33 ± 1.0</td>
</tr>
</tbody>
</table>

\[ m = \exp(\beta_0 + \beta_1 \ln(D^2H)) \]

Notes: \( \beta_x \) are linear model coefficients (\( \beta_0 \) includes CF, see text), RSEₘₐₓ is the standard error of the normalized residuals (\( m_{pred}-m_{obs}/m_{obs} \) in kg), RSE is the standard error of the residuals (backtransformed to linear units of kg), \( R^2 \) is the coefficient of determination, \( n \) is number of harvested stems, D range is range of basal diameters (cm) of harvested stems, H range is the range of heights (m) of harvested stems, \( \rho \) is mean wood specific gravity (oven-dry at 100°C) ± 95% CI standard error of the mean, and WC is wood water content as a percentage of wood green mass with 95% CI s.e.m.

† A second generic equation was created using \( \rho D^2H \) as a predictor variable in place of \( D^2H \), where \( \rho \) is the species-specific mean \( \rho \) using values from above.

†† A third generic equation was fit with several additional empirical terms to minimize residual error (see Colgan (2012, in prep) for additional information):

\[ m = 0.110d^{(1.38+0.15\ln(d))}h^{0.73}\rho^{0.80} \]
Fig. 13. Woody species composition by basal area (BA) for Kruger National Park (~2 Mha). Fractional BA was measured from n = 101 field plots located throughout the park in 2008, which was then aggregated within each vegetation class of Venter (1980). The final contribution of each species was determined by multiplying each veg class by its areal cover from Venter’s vegetation map of KNP.
Fig. 14. Species-specific stem allometry relating harvested wood mass (oven-dry) to stem diameter. Note $R^2$, CV, and e are based on backtransformed data in linear units (i.e. in units of kg) which includes the correction factor. Error bars represent measurement error (95% CI).
Fig. 15. Species-specific stem allometry relating harvested wood mass (oven-dry) to the compound variable of D^2H. Most fits improved (RSE, R^2) relative to stem diameter alone.
Fig. 16. a) Wood specific gravity and b) wood water content by species.
Fig. 17. Water content (WC) as a function of stem diameter for each species. Black points indicate basal WC measurements; red points indicate total tree WC using a weighted mean of multiple WC samples per tree, use mass of each branch size class as the weighting factor. Regression statistics are only shown for statistically significant regression slopes; although basal WC decreases with increasing size for most species, total tree WC only changes for two species.
Fig. 18. Comparison of stem water content (WC) to wood density (expressed as wood specific gravity (ρ)) for all stems where these information were available. The analytic expression shown was derived using the definitions of WC and ρ, assuming all volume not occupied by water is occupied by cellulose (specific gravity ≈ 1.5).

\[
WC = \frac{1 - \frac{WSG}{1.5}}{WSG + \left(1 - \frac{WSG}{1.5}\right)}
\]

\[R^2 = 0.65\]
Fig. 19. a) Harvested stem mass linearly correlated to cylindrical volume for five dominant species in KNP, computed using the species-specific allometry converted to units of m$^3$ (shaded regions are 95% CI bands from the data in Fig. 3) b) mass vs. estimated cylindrical mass, with each point computed as stem volume multiplied by its sampled $\rho$ (instead of species-mean $\rho$), then the regressions were re-computed. The slope in (a) can be defined as the form factor F (taper) multiplied by $\rho$, whereas the slope in (b) represents taper only.
References


Brady, J. R. 1955. The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology. University of Wisconsin.


Gray, H. 1956. The form and taper of forest-tree stems. IFI.


