

## Tree allometries reflect a lifetime of herbivory in an African savanna

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**Abstract.** Theories of plant allometry provide a general description of allometric scaling that is supposedly applicable across a wide array of environmental conditions. Scaling theories, however, ignore disturbances such as herbivory in their derivation. Here we examine the influence of herbivores on the scaling of height and diameter of two common African savanna tree species. Using Bayesian piecewise regressions, we show that herbivores modify tree allometry. We also show that the pattern of allometric modification contains information regarding herbivore foraging behavior and the resultant alteration of plant architecture. Interpreting realized allometries in the light of theoretical predictions based on assumptions of zero disturbances may help reveal the degree of herbivore impacts. However, predictions of plant form and function that fail to include disturbances such as herbivory may struggle to find general applicability.

**Key words:** allometry; Bayesian piecewise regression; browsing; herbivory; savanna; scaling exponents.

### INTRODUCTION

The relationship between the magnitude of two organism's traits or organs is often described by the equation  $Y = Y_0 X^b$ , where  $Y_0$  is a normalization constant and  $b$  is the allometric scaling exponent, describing how  $Y$  changes in relation to  $X$ . In plant ecology, a large body of theory uses this framework to examine the mechanisms governing the scaling of plant form, linking structure to the dynamics of internal resource supply or external physical limitations. These theories often seek to predict how stem height and diameter should scale with one another in trees, and therefore provide theoretical expectations for the scaling exponent  $b$  (McMahon and Kronauer 1976, West et al. 1999, Niklas and Spatz 2002, Price et al. 2007). Predictive models of plant height–diameter allometry can be categorized into two groups: those based on mechanical constraints (e.g., McMahon and Kronauer 1976, Niklas 1992), and those based on metabolic and hydraulic limitations (e.g., West et al. 1999, Niklas and Spatz 2004, Price et al. 2007). The preeminent models in both set of theories (i.e., “elastic similarity” model [McMahon and Kronauer 1976];

“fractal branching network” model [West et al. 1999]) predict that height should scale with diameter with a scaling exponent  $b$  of 2/3.

The utility of these theories has been widely criticized (Coomes 2006), as often empirical data do not match the theoretical predictions (e.g., Muller-Landau et al. 2006) and contextual factors are overlooked (Henry and Aarssen 1999). However, making comparisons between observed scaling exponents and theoretical predictions can yield information on how trees differ in form from architectures designed to optimally cope with mechanical and hydraulic constraints. Moreover, comparing allometry between populations can highlight important architectural and ontogenetic differences and the environmental drivers causing them. This is particularly true for the allometry between stem diameter and tree height because of the importance of height for light capture in forests and escape from fire and herbivores in savannas. Interspecific variability around predicted scaling exponents has been interpreted as a result of differences in species-specific resource allocation patterns in response to the light environment (O'Brien et al. 1995). Intraspecific variation in scaling exponents is often observed and has been attributed to factors such as stand age, stand density, and neighbor effects (Henry and Aarssen 1999, Henry and Thomas 2002, Kaianiemi and Lintunen 2008).

Manuscript received 8 February 2011; revised 27 May 2011; accepted 1 June 2011. Corresponding Editor: T. P. Young.

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The role of disturbance has been understudied in the interpretation of plant allometry (but see Archibald and Bond 2003, Coomes et al. 2003). Browsing disturbs bud banks and ultimately results in modified plant growth and architecture. These architectural changes may be reflected in stem diameter–height allometry, as changes in diameter growth are unlikely to be of the same magnitude or even in the same direction as change in height (e.g., Dharani et al. 2009).

Traditionally, studies have used size-class distributions to investigate browser impact on tree populations (e.g., Pellew 1983, Asner et al. 2009). These size distributions reflect modification by browsers but are also subject to environmental variations. Direct measurements of height growth over time can reveal similar impacts, but such data necessitate large sampling effort and repeated measurements. Here we used stem diameter–height allometries to investigate browser impacts. We examine changes induced by two megaherbivore browsers, African elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*), on two regionally dominant savanna trees and compare our results to theoretical predictions. We also compare allometric scaling exponents between impacted and unimpacted populations to explore both the degree of browser impact and the validity of theoretical predictions in the presence and absence of browsers.

## METHODS

### Study areas

All sampling was conducted in November and December of 2008 and 2009 within the Kruger National Park, South Africa on *Acacia nigrescens* Oliv. and *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J.Léon. *Acacia nigrescens* is heavily eaten by giraffe and is abundant throughout the southern regions of Kruger National Park (see Plate 1). *Colophospermum mopane* forms extensive monodominant stands throughout the northern regions of the park, and is the staple forage for elephants through the dry season in this region (Codron et al. 2009). *Acacia nigrescens* was sampled at two sites exposed to herbivory: Satara (24.99 S, 31.50 E) and Makhohlola (25.24 S, 31.90 E). The data collected at these two sites were combined and all subsequent analyses done on the pooled data set. The site at Makhohlola is paired with a 2.4-ha long-term herbivore enclosure established in 1974. *Colophospermum mopane* was sampled in and around the 309 ha ‘Nwashitsumbe enclosure (22.77 S, 31.27 E). Both of these enclosures are designed to exclude all mammalian herbivores larger than a hare (~5 kg). Within each species, all populations sampled were exposed to similar fire return intervals (*C. mopane*, mean 4.4 years; *A. nigrescens*, mean 5 years) over the past 30 years, despite short-term fire manipulation experiments within the

Makhohlola enclosure (van Wilgen et al. 2000, Asner et al. 2009).

### Sampling

At each site outside of an enclosure and within the ‘Nwashitsumbe enclosure multiple transects were walked and stem diameter of the largest stem at 10 cm above ground level was measured for each *A. nigrescens* and each *C. mopane* individual encountered within 5 m either side of the transect line. For trees <20 cm in height, diameter was measured at ground level. Each transect was 2400 m long within and outside of the ‘Nwashitsumbe enclosure, 200 m outside of the Makhohlola enclosure, and 2500 m in Satara. Transects were repeated at each site until at least 200 individuals of each species at each site had been sampled. Due to their rarity in the landscape active searching for *A. nigrescens* and *C. mopane* individuals >10 m in height or 40 cm in diameter was conducted. All *A. nigrescens* individuals within the 2.4-ha Makhohlola enclosure were sampled due to its small size. Height was measured to the nearest centimeter using a measuring tape for trees below 2 m. The height of trees taller than 2 m was measured using a clinometer to the nearest half-degree inclination (~0.5 m for the largest trees sampled).

Two megaherbivore browsers are particularly influential in this system. *Acacia nigrescens* is heavily utilized by giraffe and *C. mopane* by elephant. Here we focus specifically on the interaction of *A. nigrescens* with giraffe, and *C. mopane* with elephant. *Colophospermum mopane* is not eaten by giraffe (Redfern et al. 2006). We excluded *A. nigrescens* clearly targeted by elephants (e.g., snapped branches, stripped bark). It is not, however, possible to discern more subtle signs of elephant visitation (e.g., leaf pruning) on *A. nigrescens*, and thus we cannot completely eliminate the influence of light elephant browsing.

### Data analysis

The statistical analyses were performed using a Bayesian framework. The change in growing conditions occurring when a tree grows beyond the reach of a browser represents a natural system breakpoint. This breakpoint should be reflected in the height–diameter allometry. Piecewise models were used to identify these breakpoints within the tree allometry data set (Toms and Lesperance 2003, Beckage et al. 2007). Both single and double breakpoint models were tested and the best model selected using the deviance information criterion (Spiegelhalter et al. 2002) (see Appendix A for a full description of model equations and fitting). Models were fitted using Markov chain Monte Carlo algorithms implemented in WinBUGS 1.4 (Lunn et al. 2000). Diagnostic analyses were performed in R 2.11.0 (R Development Core Team 2010).

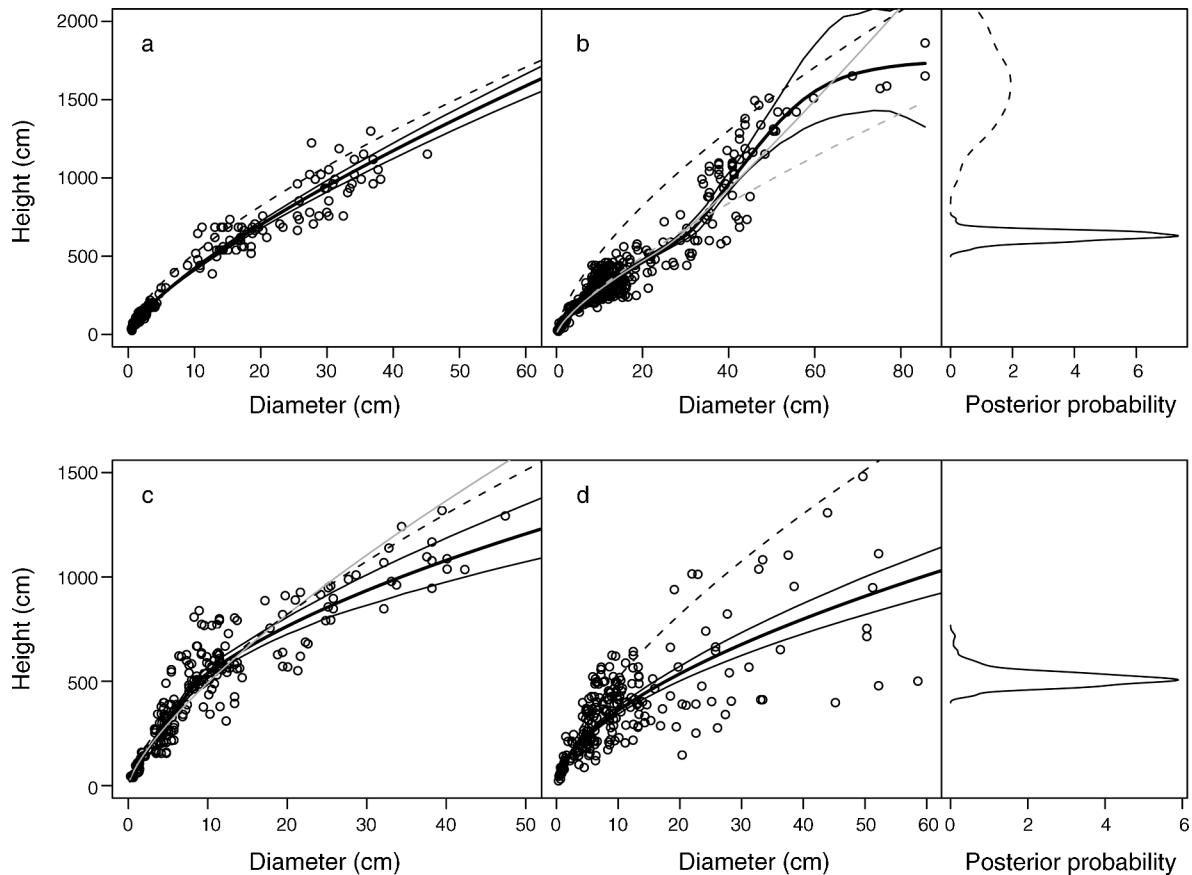


FIG. 1. Fitted height–stem diameter allometries for *Acacia nigrescens* (a) protected from herbivores and (b) exposed to herbivores, and for *Colophospermum mopane* (c) protected from and (d) exposed to herbivores. Thick solid black lines show the best-fitting models. In panel (b) the dashed gray line shows the curve fitted when using a simple linear model, and the solid gray line shows the fit using a single breakpoint model. In panel (c) the solid gray line shows the fit using a simple linear model. Thin solid lines show 95% credible intervals surrounding means. The dashed black line shows the prediction from mechanical theory of elastic similarity, with parameters from Niklas and Spatz (2004). Posterior densities for breakpoints in panels (b) and (c) are shown. Back-transformed model results are shown after fitting in log–log coordinates.

## RESULTS

Parameter estimates for all fitted models and their credible intervals are given in Appendix B: Table B1. The best-fitting models for *A. nigrescens* were a simple linear model for the protected population and a two-breakpoint model for the population exposed to herbivores (Appendix B: Fig. B1a and b). In this latter case the first breakpoint occurred around a height of 620 cm, an estimate that was relatively well defined (95% credible interval 520–680 cm). The second breakpoint was poorly defined at 1560 cm (95% credible interval 1010–2190 cm) due to the paucity of data above it. For *C. mopane*, a simple linear model fitted the exposed population best and a model with a single breakpoint at 510 cm (95% credible interval 440–590 cm) fitted the population within the enclosure best (Fig. 1c and d). Here we describe only the best-fitting model for each population.

For *A. nigrescens* the scaling exponents were generally greater than theoretical predictions of  $2/3$ , both when protected (0.74) and when exposed (0.71 and 1.54, respectively, before and after the first breakpoint) to herbivores (Appendix B: Fig. B1). In the latter situation the scaling exponent decreased drastically (0.07) after a second breakpoint, but this estimate was unreliable (Appendix B: Fig. B1).

For *C. mopane*, most exponents of the exposed population also exceed predicted values. The scaling coefficients of simple linear models were very different between populations inside and outside of the enclosure (0.74 inside and 0.57 outside; Appendix B: Table B1 and Fig. B2). When the piecewise model was used for the protected population the slope before the breakpoint was 0.85 and 0.50 after the breakpoint (Appendix B: Fig. B2).

As diameter increases, so does the modeled difference in height between *C. mopane* populations protected from, and exposed to, herbivores (Fig. 2). Height

differences between the protected and exposed population of *A. nigrescens* also increased as diameter increased, until the first breakpoint in the allometry of trees exposed to herbivores. For larger *A. nigrescens* trees, as a result of an increase in the scaling exponent of exposed trees, height difference decreases toward zero.

#### DISCUSSION

Herbivores appear to have a strong influence on height–diameter allometry and population-level patterns of herbivore impact are evident in the modified allometries. Trees exposed to herbivory have a much lower height for a given stem diameter. In the population of *A. nigrescens* exposed to herbivory we observed breakpoints in the measured allometry, with a noticeable shift around 520–680 cm, which is just above the limit to which giraffe have been reported to browse (Pellew 1983, Young and Isbell 1991, Bond and Loffell 2001). This breakpoint and the high scaling exponent observed after the breakpoint suggested that trees that eventually escape from the influence of giraffe grow quickly in height toward unmodified allometry. This could occur because the alteration of allometry is likely a result of reduced height growth from the repeated browsing of branch tips. When the highest branch tips are beyond the reach of giraffe, height growth can begin to recover (Pellew 1983). The unexpected support for the addition of a second breakpoint near the maximum tree size observed and the decrease in the scaling exponent above it suggests different constraints operating near maximum tree height.

Conversely, it appeared that there was no invulnerable size range within *C. mopane*, with the largest sampled trees showing the greatest degree of modification. This is evident in the pattern of increasing architectural modification with size in Fig. 2, reflecting that elephants are capable of breaking stems up to 60 cm in diameter. In the population of *C. mopane* protected from herbivory height increased rapidly with diameter for smaller individuals until a breakpoint 440–590 cm in height, after which the scaling exponent decreased. *Colophospermum mopane* is a multistemmed shrub initially, both in the presence and absence of herbivores, with a single stem eventually dominating as the plant develops into a large tree (Hempson et al. 2007). The observed breakpoint and concomitant change in scaling exponent is possibly the result of a transition from multi- to single-stemmed form. Strong inter-ramet competition is likely when the plant is highly multistemmed, perhaps resulting in the high scaling coefficient observed before the breakpoint (Henry and Aarssen 1999, Poorter et al. 2006).

Factors other than herbivory can affect height–diameter allometry, such as neighbor density and local light conditions (Henry and Aarssen 1999). Previous studies at our study sites have shown that plant density and canopy cover is greatly lower outside the exclosures,

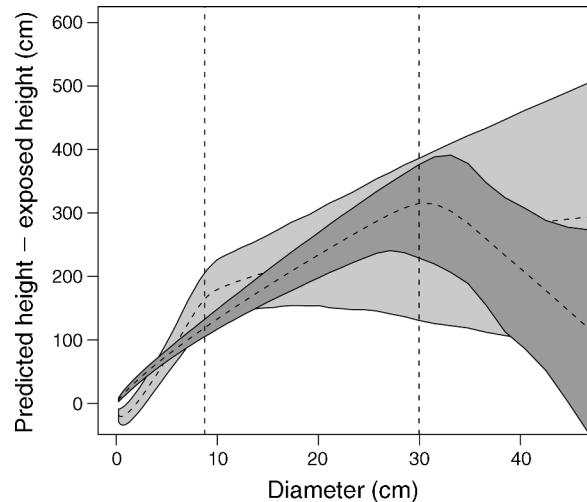


FIG. 2. Predicted differences in height at a given diameter between populations exposed to and protected from herbivores for *Colophospermum mopane* (light gray) and *Acacia nigrescens* (dark gray) using the best-fitting models for each species. The shaded areas show the 95% credible interval surrounding the mean (dashed curves). Dashed vertical lines show the position of the first breakpoints for *C. mopane* at 8.8 cm and *A. nigrescens* at 30 cm.

where trees taller than 4 m become rare and isolated (Asner et al. 2009, Levick et al. 2009). Thus it is possible that the differences observed here between population exposed to and protected from herbivores are confounded by differences in density. However, evidence from field observations (architectural modification of isolated browsed *A. nigrescens*, clear identification of tree snapping by elephants for *C. mopane*) attests to the dramatic direct impact of herbivores. In semiarid savannas it is also unclear how neighbor competition would affect the relative growth of height and diameter growth as competition may mostly occur belowground, and this warrants future research. Pruning and thinning experiments should allow disentangling between density and direct browsing effects in allometry, but to the best of our knowledge have not been conducted over a long enough period of time and analyzed in terms of height–diameter allometry.

In most cases scaling exponents were somewhat higher than the predicted 2/3 from mechanical or hydraulic considerations (McMahon and Kronauer 1976, West et al. 1999, Niklas and Spatz 2004). Most data sets used to test allometric theories of tree structure do not include savanna trees (e.g., Niklas and Spatz 2004, Muller-Landau et al. 2006). The importance of stem diameter in determining the vulnerability of stem tissue to heat damage (Lawes et al. 2011), and the importance of tree height in elevating canopy bud banks above flame height or maximum height of herbivory (Trollope 1984, Bond 2008) may result in trees



PLATE 1. A fence-line contrast at the Makhohlola enclosure in southern Kruger National Park showing *Acacia nigrescens* exposed to herbivores (left) and partially protected (right). Note the similarity in diameter and difference in height of the two trees in the front of the frame. Photo credit: G. R. Moncrieff.

compromising on mechanical stability or hydraulic efficiency. If true, it would suggest that the decreased height for a given diameter caused by herbivory, as observed in this study, may have important consequences for ongoing vulnerability to fire or herbivory. Shorter trees may stand a better chance of surviving a fire as a result of thicker stems and hence thicker bark.

Using stem height–diameter allometry to quantify browser impact has several advantages: the data can easily be acquired for many individuals facilitating comparison between populations across broad spatial scales, herbivore impact on allometry reflects the entire lifetime of disturbance to the growth of plants across a wide size range, and, as we have shown, the pattern of alteration may contain information regarding the nature of the herbivore’s foraging behavior. A critical aspect is to disentangle between herbivore effects and those from other factors. Here we relied on an unreplicated enclosure set-up, but mechanistic models of tree growth and architecture under competition and disturbance would provide useful theoretical predictions and allow testing contrasted hypotheses of tree growth limitations and tree strategies to cope with them. However, competition and disturbances are currently virtually absent of allometric models of optimal architecture (Coomes 2006). Finally, the implications of allometric changes under herbivory for plant fitness and demography will have to be understood. Long-term monitoring

of individual trees will be useful, but we also suggest that short-term response to experimentally caused disturbance (e.g., fire) of trees of different allometry may bring valuable knowledge in a short period of time.

Ultimately, it is important to note that the “modified” allometries of trees exposed to herbivores reported in this study do not represent aberrations. Indeed, the allometries of trees protected from herbivores within enclosures represent more atypical cases in African savannas with an intact mammal fauna. A general predictive theory of plant form and functioning that does not account for the variation introduced by natural disturbance agents, such as herbivory, may prove to be neither general nor predictive in systems with frequent disturbances.

#### ACKNOWLEDGMENTS

Funding was provided by the National Research Foundation of South Africa, the University of Cape Town, and the Biodiversity and Climate Research Centre, BiK-F (which is supported by the “LOEWE—Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz” program of Hesse’s Ministry of Higher Education, Research and the Arts, Germany). We also thank two anonymous reviewers for constructive feedback.

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#### APPENDIX A

Models used and fitting of Bayesian piecewise regressions (*Ecological Archives* E092-200-A1).

#### APPENDIX B

A summary of fitted models and parameters with figures of estimated scaling exponents (*Ecological Archives* E092-200-A2).