

The architectural design of trees protects them against large herbivores

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Summary

1. Where large browsers are abundant, the survival of trees depends on their ability to deploy defences, either chemical or structural. Structural defences include the arrangement of dense and intricate architecture, termed 'cage' architecture. Previous studies showed that trees developing in herbivore-rich environments tend to have more cage architecture but its precise effect on mammalian herbivores remains unknown.
2. In this paper, we experimentally test how cage architecture affects the bite rate of goats, a generalist mammalian herbivore.
3. We selected 11 palatable tree species with contrasting architectures. We described their caginess using an index combining spinescence and woodiness of their stems. Finally, we evaluated how the caginess of trees slows down herbivores when feeding on the inner leaves in tree crowns.
4. We observed that the bite rate of goats on inner leaves of the cagiest trees was so severely reduced that they could not satisfy their daily nutritional requirements. We discuss how this could affect the preference of wild herbivores for less cagy trees, especially at the end of the dry season.

Key-words: plant architecture, structural defences, herbivory, cage architecture, spinescence, bite rate

Introduction

In many ecosystems large mammalian herbivore (hereafter, large herbivores) populations affect the composition and structure of plant communities (Skarpe 2001; Côté *et al.* 2004; Greve *et al.* 2012), and can in places, become one of the primary factors determining plant species abundance (Martin *et al.* 2010; Midgley, Lawes & Chamaille-Jammes 2010; Staver *et al.* 2012). Herbivores tend to select plants with high concentrations of nutrients and/or low concentrations of secondary metabolites (Cooper, Owen-Smith & Bryant 1988; Hanley & Lamont 2002; Owen-Smith 2002; Bedoya-Pérez *et al.* 2014; DeGabriel *et al.* 2014). The role of chemical defences in plant–herbivore interaction is well accepted, but herbivores additionally favour plants that allow for fast feeding rates. Plants that reduce intake rates, either due to reduced bite size (e.g. small leaves) and/or bite rate (e.g. spinescence), are generally less favoured

(Cooper & Owen-Smith 1986; Belovsky *et al.* 1991; Milewski, Young & Madden 1991; Grubb 1992; Gowda 1996; Charles-Dominique, Midgley & Bond 2015).

Spinescence has been the main focus of studies that have investigated how plants can physically impair mammalian herbivore foraging (Cooper & Owen-Smith 1986; Hanley *et al.* 2007; Skarpe *et al.* 2012; Pérez-Harguindeguy *et al.* 2013; Burns 2014). Surprisingly, the idea that the whole-plant structure, that is, the branching organization, might affect how and to what extent herbivores can forage a tree, and thus act as a defence trait, had until recently received little attention. Bond, Lee & Craine (2004) and Bond & Silander (2007) showed how the divaricate branching could be a legacy of the evolutionary influence of extinct moas in New Zealand and reduce the feeding rate of similar birds, such as ostriches and emus. In African savannas, Archibald & Bond (2003) showed that *Acacia karroo* trees growing in environments with high herbivore pressure have a short and wide canopy with a high branching density, thus forming a 'cage' architecture. Staver *et al.* (2012) showed

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for nine *Acacia* species that their relative position on a trade-off axis between fire and herbivory depends on their branching density. Several studies therefore point towards an effect of whole-plant structure in limiting browsing, but this hypothesis lacks experimental support.

Our study addresses this gap by testing the effect of plant structure on the bite rate of large herbivores, and investigates what developmental traits contribute to ‘caginess’. The branching density of a plant has been used to describe the caginess of a tree (Archibald & Bond 2003; Staver *et al.* 2012). Branching density is a highly variable trait, changing with age, position in canopy, browsing history, fire history, access to light, plant vigour, disease and water stress (Pérez-Harguindeguy *et al.* 2013). Because of this high variability, a plant species cannot be described by a single value of branching density but rather by measurements in different populations along the environmental gradient of interest (as in Archibald & Bond 2003; Pérez-Harguindeguy *et al.* 2013), for instance, from low to high herbivore pressure. This variability complicates the use of branching density in analyses comparing across a large set of plant species at the community scale. Finding morphological traits, other than branching density, that are stable at the species level, and that describe the ‘caginess’ of a plant, is thus a pre-requisite for a sound analysis of the relationship between whole-tree architecture and browsing.

Trees have a modular organization but all their branches do not have equivalent morphological properties. The branches composing the shoot system of a tree can be grouped according to their morphological properties into a limited number of axis categories (e.g. main stem, branch, twig, short shoot), generally up to four for broad-leaved species and up to six for Conifer species (Edelin 1977; Hallé, Oldeman & Tomlinson 1978; Grosfeld, Barthélémy & Brion 1999; Barthélémy & Caraglio 2007). The huge number of stems that makes up the shoot system of a large tree is achieved by repeatedly duplicating shoot systems composed of these axis categories through a process called reiteration (Barthélémy & Caraglio 2007). The relative arrangement of modules (Fig. 1) defines the dimension of the crown, whereas the properties of axis categories determine the relative investment of the plant in different functions. For example, many plant species have their first axis category (trunk for trees) specialized for exploration, and peripheral axis categories specialized in assimilation and reproduction (Barthélémy & Caraglio 2007). In species such as spiny *Acacia*, not all axis categories are contributing to protection: most of the South African *Acacia* (*sensu lato*, *Vachellia* and *Senegalia*) have spiny trunks and branches but have also short shoots that produce flowers; 2–10 leaves per year and do not produce any spine (T. Charles-Dominique, pers. obs.). The number of axis categories is genetically fixed at the species level (Barthélémy & Caraglio 2007) and thus provides an accurate tool to compare species’ abilities along environmental gradients. In this paper, we hypothesize that the number of spiny and woody axis categories (Fig. 1) greatly determines the

caginess of a tree and thus can be used to build an index that could estimate to what extent the whole-tree structure contributes to protect the tree against large herbivores. The number and arrangement of modules could also contribute to caginess, but vary with plant age and have a high intraspecific variability (Charles-Dominique, Staver *et al.* 2015).

We tested this hypothesis by estimating goat (*Capra hircus*) bite rate on 11 savanna trees of contrasting architectures. For each tree species, we described the architecture and indexed the caginess by considering the number of axis categories that are woody and/or spiny. The effect of caginess on goat bite rate was determined by comparing bite rate between whole trees and isolated branches. We predicted that this difference would be positively related to caginess, hence indicating that whole-tree architecture has the potential to influence mammalian browsing rate.

Materials and methods

STUDY SITES AND SELECTION OF PLANT SPECIES

Experiments were conducted at the experimental farm of the Owen Sithole College of Agriculture (Empangeni, South Africa), where goats are commonly used in the study of herbivore foraging. In this study, we used 20 young castrated male goats. The goats were not fed on the morning preceding the experiments.

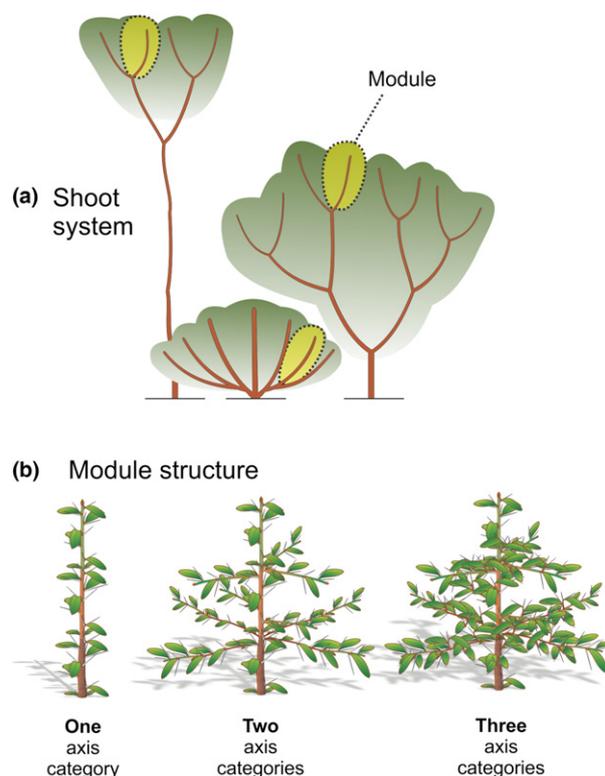


Fig. 1. Examples of plant organization. (a) Shoot systems with the same module structure but with varying features of reiteration. (b) Modular unit with one, two and three axis categories. The first axis category is orthotropic, spiny and conic; the second axis category is plagiotropic, spiny and cylindrical; the third axis category is ageotropic, spiny and cylindrical.

Plants used in this study were sourced from Hluhluwe-iMfolozi game reserve (hereafter HiP), KwaZulu-Natal province, South Africa. There vegetation ranges from *Acacia*-dominated savannas to treeless grasslands at the highest elevations and includes broad-leaved thickets and tall forests (Whateley & Porter 1983). Large mammalian herbivores are abundant and the browser and mix-feeder guild is particularly diverse, including impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), elephant (*Loxodonta africana*), zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), black rhinoceros (*Diceros bicornis*), kudu (*Tragelaphus strepsiceros*), red duiker (*Cephalophus natalensis*) and grey duiker (*Sylvicapra grimmia*). Among these, species from the medium-sized mixed feeder guild, such as impala, are likely to have been one of the strongest selective forces behind the evolution of structural defences such as spinescence (Charles-Dominique *et al.* 2016). However, using wild animals in controlled experiments is difficult. For this reason, goats are frequently used as a surrogate for wild medium-sized browsers. The bite sizes of goat, impala, common duiker and bushbuck (*Tragelaphus sylvaticus*) have been found to be relatively similar, while kudu bite off larger stem diameters (Cooper & Owen-Smith 1986; Wilson & Kerley 2003).

For this study, we initially selected 25 of the most frequently found tree and shrub species in HiP. We conducted a preliminary cafeteria experiment to assess the palatability of the different species to goats. Among the 25 species, we excluded six species (*Celtis africana*, *Grewia flavescens*, *Spirostachys africana*, *Diospyros natalensis*, *Plectroniella armata* and *Diospyros dicrophylla*) that were either left untouched by goats at the end of the cafeteria experiments or least preferred during the trials. We excluded these species to ensure that all the species used are considered acceptable by goats and that our observations on foraging rates were not affected by the plant being unpalatable. Out of the 19 remaining species, we then selected 11 that had contrasting architectures. The 11 selected species are listed in Table S1, Supporting Information.

ESTIMATION OF THE EFFECT OF TREE ARCHITECTURE ON HERBIVORE BITE RATE

We first estimated a once-off baseline measurement of goat bite rate when browsing isolated branches. For each plant species, we collected five branches (of c. 1 m in height) from five different trees and placed them onto a grid, isolated from each other (Fig. S2b). One goat (randomly chosen from the 20 available) was introduced and allowed to take 50 bites from the branches. The goat was then replaced by another (also randomly chosen) that was also allowed to forage for 50 bites. The process was repeated until 200 bites had been taken (i.e. four goats). Bite rate was calculated from the time needed by goats to obtain these 200 bites. The value of 200 was chosen to ensure that many leaves remained on each branch and that any change in bite rate was not due to reduced leaf availability. We also recorded the time every 10 bites, which allowed us to visually verify that our results were not affected by a few extreme bouts of very quick or very slow bite rates.

With this design, the baseline bite rate was estimated from five isolated branches browsed by four different goats, thus limiting the bias that could have been introduced by unusual branch morphologies or individual differences in goat browsing rate. We also estimated the average goat bite size on each tree species by weighting isolated branches before and after browsing, and dividing the difference by the number of bites taken.

Second, we estimated goat bite rate when browsing inside the crown of whole trees, using three replicates per species. For each plant species, we collected three saplings (c. 1 m tall and 1 m wide). We removed the peripheral leaves, that is, those located in the outermost layer of the canopy (c. 30 cm) from each sapling before offering the sapling to the goats. Removing peripheral leaves forced goats to feed well within the tree crown and allowed

us to contrast bite rates with (at the centre of the crown) and without (on isolated branches) the cage effect. As stated earlier, successive goats were allowed to take 50 bites, until no leaves were available or accessible. The bite rate in the crown was estimated from the time needed by goats to obtain the last 200 bites. Again, we recorded the time every 10 bites to check for the presence of outlier values (see boxplots of Fig. 2). This visually revealed variability between and within trees, although the sample size was too low to conduct a robust statistical analysis on this. For each tree, we calculated a relative bite rate per species as the difference between the 'whole tree' bite rate and the 'isolated branch' bite rate. Values <0 indicate faster foraging on isolated branches than on whole trees and vice versa. We finally tested, using linear regression, whether this relative bite rate could be explained by the plant investment in structural defences (ISDs).

ARCHITECTURAL ANALYSIS OF SELECTED SPECIES

The architectural analysis was performed according to the concepts and methods recently revisited by Barthélémy & Caraglio (2007). The method consists of grouping all stems (i.e. trunk, branches, twigs and short shoots) in the plant body into axes with similar morphological properties. This then highlights duplicated structures (reiteration) within the plant body. When describing plant axis categories (*sensu* Barthélémy 1991), the morphological descriptors prescribed for the architectural analysis were based on the following diagnostic descriptors: growth direction (plagiortropy/orthotropy/mixed), stem shape, length of internodes (portion of stem between two consecutive leaves) and mode of branching (sub-apical/acrotonic/mesotonic/basitonic). Stem shape was assessed by evaluating the difference between basal [i.e. near the ground (for trunk) or insertion point (for other stems)] and distal (i.e. near the stem apex) diameter. A stem was considered cylindrically shaped if this difference was <20%, conic otherwise. The length of the internodes was described in three categories: long internodes for axes where the longest internodes were 2 cm or longer, short internodes for axes where the longest internodes were between 0.2 and 2 cm and very short internodes for axes where all internodes were shorter than 0.2 cm. We noted the ability of each axis category to bear a lateral spiny organ with a sharp tip (thorn, spine, hook). The results are presented in the form of an architectural table (Table S1; Fig. S1).

INVESTMENT IN STRUCTURAL DEFENCES

For each plant species we constructed a score of the plant's ISD. We first conducted observations of impala and goat browsing. These observations suggested that two properties of axes were mainly contributing to prevent them from accessing leaves in the inner part of the crown: spines and conic stems. For the set of plant species studied here, the concity of an axis category directly corresponds to the fast rate of wood development in a stem. We postulated that spinescence brings a more efficient protection against herbivores than woodiness. We thus gave a more important weighting to the presence of spines compared to the woodiness in our index. Thorns were considered as lateral spines on their bearing axis. For a particular architectural unit, we scored the ISD as follows:

$$ISD = \prod_{i=1}^n (1 + 2^i s_i + 1 \cdot 2^i c_{i+1})$$

with i the rank of the axis categories ordered from the inside of the species' architectural unit to the periphery, s_i is the presence of spines borne by an axis category i (1 = presence; 0 = absence) and c_i describes the concity of the axis category i (1 = conic; 0 = cylindrical).

Any axis category that is not bearing a conical axis category or not spiny is not contributing to the investment in defences.

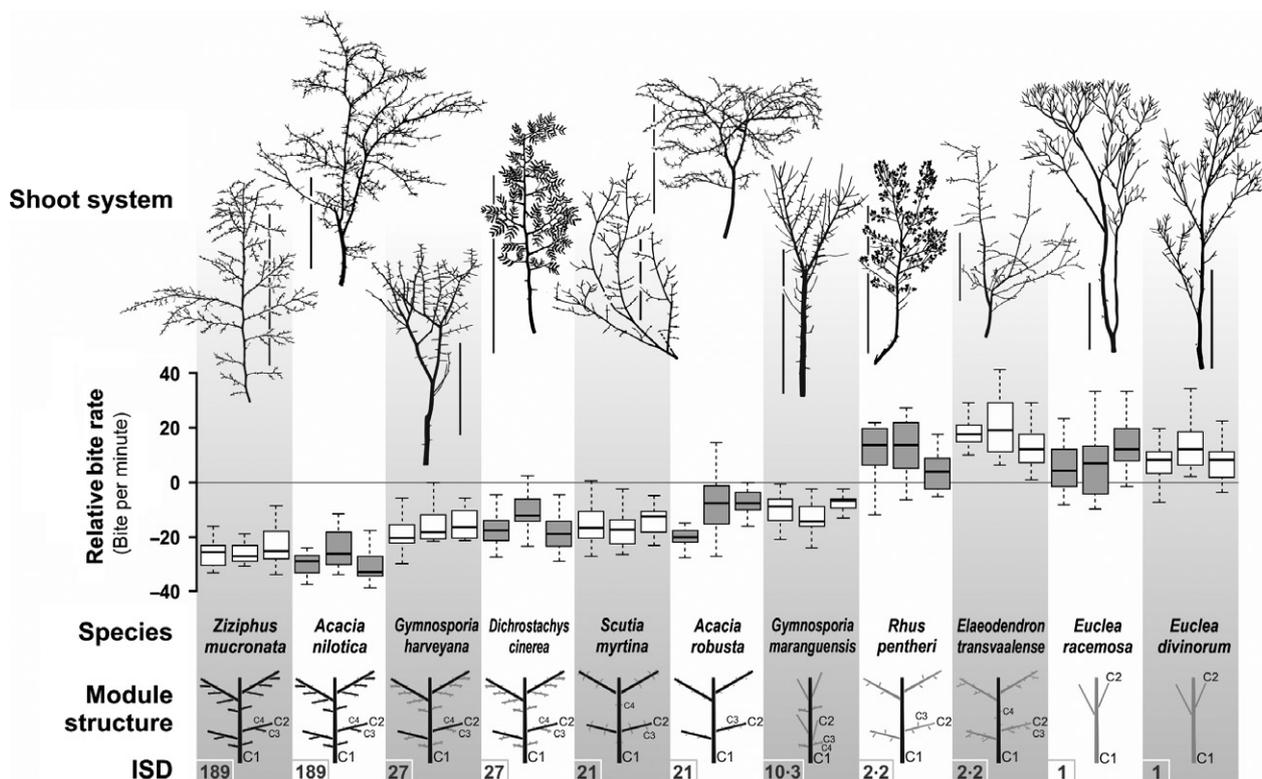


Fig. 2. Species architecture and bite rate of goats. The relative bite rate shows the difference between goat bite rate inside the crown (with cage effect) compared to goat bite rate on isolated branches (without cage effect). Negative (c. positive) values indicate that goats feed more slowly (c. rapidly) inside of the crown than on isolated branches. Each boxplot summarizes the values obtained for each of the three saplings used per species (i.e. the variation in relative bite rates over increments of 10 bites. See text for details). A black stem in the 'Module structure' has its leaves protected by spines and/or lateral woody branches; Leaves borne on grey stems are not protected. The morphological properties of axis categories 'C1', 'C2', 'C3' and 'C4' for each species are presented in Table S1. 'ISD' is the 'investment in structural defence' Index.

Figure 1b illustrates three theoretical architectural units consisting of one, two and three axis categories, with the first axis category orthotropic, spiny and conical, the second axis category is plagiotropic, spiny and cylindrical and the third axis category is ageotropic, cylindrical and spiny. It is important to notice that axis categories are not equivalent to branching order: short shoots can for example be born on both trunk (order 2) and main branches (order 3).

Results

BITE SIZE AND BITE RATE

Six of the 11 species (*Acacia nilotica*, *Dichrostachys cinerea*, *Gymnosporia harveyana*, *Gymnosporia maranguensis*, *Scutia myrtina* and *Ziziphus mucronata*) induced a clear 'cage effect' on goat bite rate, which was slower inside the crown of the three intact saplings than on isolated branches (Fig. 2; Tables S2 and S3). *Acacia robusta* also induced slower bite rates within the crown but for only two out of the three saplings tested. The strength of the cage effect varied greatly across this set of species, however, (Fig. 2): The cage effects induced by *Z. mucronata* and *A. nilotica* were at least twice as strong as those induced by *S. myrtina* and *D. Cinerea*, for instance. The seven species mentioned above are all spiny (Table S1; Fig. S1) but they are positioned along a gradient of

caginess (Fig. 2). The four other species (*Rhus pentheri*, *Euclea racemosa*, *Euclea divinorum* and *Elaeodendron transvaalense*) did not induce a cage effect: the goat bite rate was similar, or even sometimes greater, inside the intact crown than on isolated branches (Fig. 2).

ARCHITECTURE AND INVESTMENT IN STRUCTURAL DEFENCE

The architecture of the 11 species studied is made from the repetition of an architectural unit consisting of two to four axis categories, the properties of which are summarized in the supplementary information (Table S1; Fig. S1). Therefore, species varied greatly in their ISDs, as evaluated by our index. The species with the highest ISDs, *Z. mucronata* and *A. nilotica* have three morphologically differentiated axis categories that bear spines. Their resulting structure is very intricate and covered with spines (Fig. S2). Species with the lowest ISDs, *Eu. divinorum* and *Eu. racemosa* have only two differentiated axis categories with a woody perennial trunk and short-lived cylindrical branches. These branches are self-pruned after 1 year and cannot prevent an herbivore from accessing the inside of the crown. The resulting structure is an open shoot system with clusters of leaves freely available to herbivores.

Goats have a slower bite rate inside the crown, compared to when feeding on isolated branches, when feeding on trees with high ISDs, as evaluated by our index (Fig. 3). Observations on the goat feeding behaviour during the course of the experiments suggested that this reduced bite rate was caused by the difficulty goats had to reach the leaves inside the crown when feeding on species that formed a dense cage. This difficulty of accessing leaves inside the cage caused goats to modify their behaviour: when feeding inside the crown, goats frequently flattened their ears and closed their eyes. For a few unprotected plant species, specifically *El. transvaalense* and *R. pentheri*, we observed greater goat bite rate inside the crown than on isolated branches. Overall, a higher investment in plant structural defences results in a slower bite rate for goats (Relative bite rate = 13.45^{***} [95% CI: 9.25;16.01] $- 8^{***}$ [95% CI: -9.02 ; -6.80] $\times \log_{10}$ [Index of caginess]; adjusted $R^2 = 0.88$; $P < 0.001$; Fig. 3).

Discussion

BRANCHING DESIGN OF CAGE ARCHITECTURES

Although it has been recently recognized that plants that are able to form cage architectures may be more likely to survive in environments with a high density of mammalian

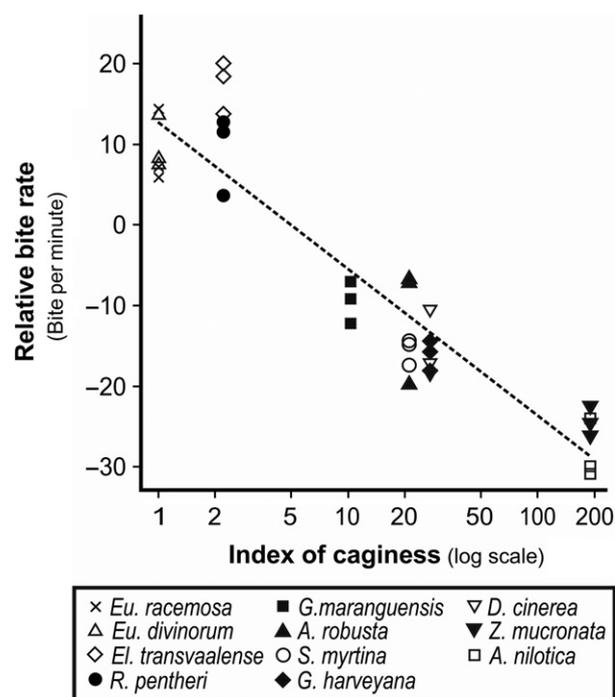


Fig. 3. Effect of caginess on goat bite rate. The relative bite rate shows the difference between goat bite rate inside the crown (with cage effect) compared to goat bite rate on isolated branches (without cage effect). Negative (c. positive) values indicate that goats feed more slowly (c. rapidly) inside of the crown than on isolated branches. Each point shows the relative bite rate per sapling ($n = 3$ for each species, see text for details). The symbols identify the different tree species. The dotted line illustrates the highly significant ($P < 0.001$) linear regression between the two variables.

herbivores (Archibald & Bond 2003; Staver *et al.* 2012), how these cages form has received little attention. From a developmental perspective, a higher branching density can be obtained either by repetition of modules with the same morphological structure ('reiteration' in Barthélémy & Caraglio 2007; Fig. 1a) or by the setting up of branches with morphologies and functions that differ from each other ('differentiation' in Barthélémy & Caraglio 2007; Fig. 1b). While the reiteration replicates the same morphological features, differentiation allows creating new functions or reinforces a given existing function. Our study revealed that the 11 tree species are built from a limited number of axis categories (up to four). We further show that, with this information as well as with information on the conicity (related to wood growth rate) of the axes and their spinescence, we could compute an index of ISDs which correlated strongly, and negatively, with herbivore bite rates within the canopy.

Characterizing the involvement of axis categories in building up a cage has several methodological and conceptual advantages, compared to measuring the branching density. First, an extensive literature in plant architecture indicates that the axis categories have stable qualitative properties (including woodiness and spinescence) at the species level (Edelin 1977; Barthélémy & Caraglio 2007) even for tree species showing exceptional phenotypic plasticity (Grosfeld, Barthélémy & Brion 1999; Charles-Dominique, Edelin & Bouchard 2010; Charles-Dominique *et al.* 2012; Charles-Dominique, Staver *et al.* 2015). The characterization of axis categories need thus only be done once for a particular species, allowing for comparisons across large sets of species along environmental gradients. In contrast, comparisons of branching density across a large set of species are complicated by the large intraspecific variation that is observed when using these metrics (Archibald & Bond 2003). The stability of axis category properties at the species level also allows for the investigation of strategy shifts of congeneric species. For example, the caginess index presented in this paper could be used to better understand why African forest trees are seldom spiny or seldom develop cagy architecture (Charles-Dominique, Staver *et al.* 2015; Charles-Dominique *et al.* 2016). We could hypothesize that the costs related to developing a cage that grows exponentially according to the number of axis categories contributing to caginess is too high in shaded environments where the light and thus assimilated income are limited.

CAGE ARCHITECTURE REDUCES HERBIVORE BITE RATES

Until now the link between whole-plant structure (i.e. caginess) and herbivore behaviour has remained untested. Here we show, using a set of 11 tree species, that this relationship holds the discrepancy in goat bite rates inside the crown and from single branches were less for plants that were not developing a cage (with an ISD <10). Testing this

relationship on intake rate rather than on bite rate only would require knowing bite size of goats when feeding at the edge or within the crowns. While practical considerations prevented us from measuring bite size accurately within the crowns, our data and observations suggests that bite size is probably reduced within the crown: bites taken at the periphery were often made by biting clumps of leaves situated near to the apices of shoots (cheek bites); bites taken within the crown were often single leaves born laterally on long shoots (front bites). As herbivores cannot crop and chew at the same time (Spalinger & Hobbs 1992; Shipley 2007), larger bites, which requires greater chewing, result in a slower bite rate. This would explain why, for species not forming a cage, bite rate was sometimes higher inside the crown. This could also apply to other trees investigated, but possibly to a lesser degree for species with very small bite sizes offered at the edge of the crown (with small leaves separated by large internodes or leaves already well protected by spines; Charles-Dominique, Edelin *et al.* 2015). This suggests that the reduction in the intake rate of mammalian herbivores inside the crown caused by cage architecture would be at least as great as that observed here on bite rate.

ECOLOGICAL IMPLICATIONS

The amount of time an herbivore has to spend feeding on a plant species to meet its daily requirement gives a good indication of how well defended the plant is (structurally

or chemically) (Cooper & Owen-Smith 1986). This is determined by the herbivore intake rate when feeding on that plant (affected by bite size and bite rate), by the availability of plants in the landscape, and also by the nutritional value of the species (Belovsky *et al.* 1991; Grubb 1992; Illius & Fitzgibbon 1994; Shipley 2007). If this feeding time is too high, an herbivore could spend a full day browsing and still remain in a negative energy budget. Additionally, extending the feeding time required to meet the daily energetic requirements can potentially have negative consequences for other behaviours ultimately affecting the fitness of animals: reproduction, time spent being vigilant for predators and in thermoregulation (Shipley 2007). Finally, intake rate should strongly influence the preference of herbivores when several plant species are available and this should also be involved in the decision of an herbivore to move from one patch of vegetation to another (Shipley 2007).

A goat can quickly achieve a daily food intake equivalent to 2.5% of its body mass (in less than 2 h spent exclusively on feeding per day) if a plant species offers large bites or is easy (i.e. fast) to harvest (Fig. 4). We consider here only the effect of structural defences: for the sake of reasoning, the removed phytomass is assumed to be of similar quality. At the periphery of the canopy, feeding rate is primarily affected by the dimensions of leaves, which affects bite size, and the presence of spines (Fig. 4, see also Cooper & Owen-Smith 1986; Belovsky *et al.* 1991; Gowda 1996; Milewski, Young & Madden 1991; Wilson &

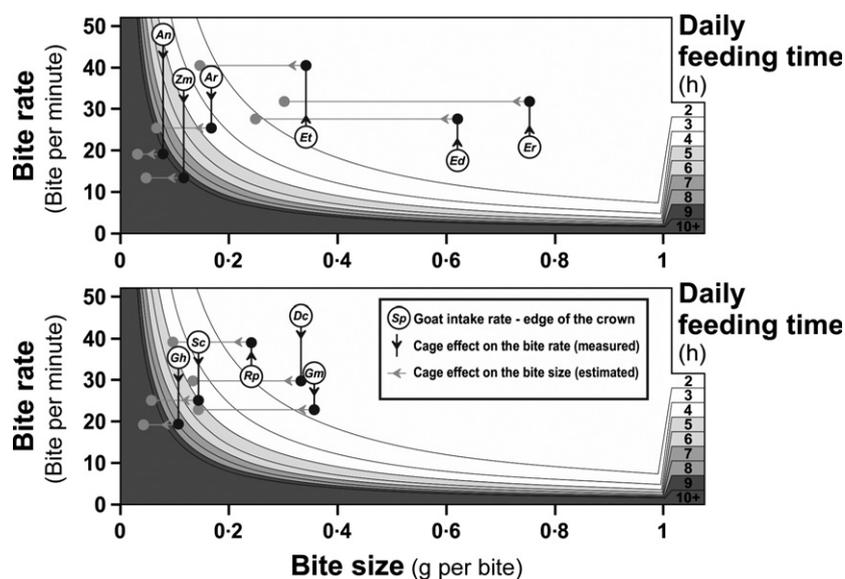


Fig. 4. Intake rates of goats and cage effects on bite rate, bite size and feeding time for the 11 tree species. This figure was made with the assumption that all plant species have similar leaf quality and thus show only the effect of structural defences. The daily feeding time is the time required by an herbivore (here a goat) to reach its daily requirement while feeding on a specific tree species; feeding time was calculated by dividing the daily requirements of the animal (in g) by the product of bite rate (bite per min) and bite size (g per bite). Open circles show the species-specific intake rate achievable at the crown periphery (as estimated from bite rates on isolated branches). Black dots show the daily feeding time necessary when forced to feed inside of the crown (at the same bite size). The grey lines simulate a potential reduction in the bite size by half inside of the crown. This was not measured in this study but was apparent during the observations of goat foraging. Goats often shifted from large cheek bites taken at the periphery of the crown to small front bites when foraging inside the tree. The herbivore will quickly fulfil its daily requirements (in less than 5 h) if feeding at a feeding rate falling within the white area but very slowly (in more than 10 h) if feeding at a feeding rate falling within the dark grey area.

Kerley 2003; Cash & Fulbright 2005; Charles-Dominique, Edelin *et al.* 2015). Our study reveals that these effects are complemented by a clear effect of cage architecture on bite rate when the herbivore feed on the inner part of the canopy. Therefore, the cage effect will mostly affect herbivore feeding time in situations where opportunities to forage only on the periphery of trees is limited (e.g. high depletion level due to few palatable trees being available, or high competition levels).

Using this framework we can show that the cage effect measured in our experiment is likely to be strong enough to impact goat performance: for *Z. mucronata* and *A. nilotica* (Fig. 4) a goat requires less than 4 h to achieve its daily requirement by feeding only at the edge of the crowns, but more than 10 h when feeding inside the cage. This result has strong implications for the understanding of the dynamic interactions between herbivores and plants. While foraging on a specific tree, the increasing time required to obtain the following bite is reducing the attractiveness of the plant for the herbivore. The diminishing rewards incentivize the herbivore to move on to a next individual thereby limiting the damage that can be caused to any particular tree. For cagy plants this means that peripheral leaves and buds would be targeted at the beginning of the growing season and progressively abandoned when the herbivore should target less palatable tree species which do not form cage architecture. In the field this is supported by the foliage left untouched inside of the cage at the end of the dry season (T. Charles-Dominique, pers. obs.).

Our results indicate that among the three components involved in building a cage (i.e. spinescence, stem woodiness and number of axis categories contributing to the cage), spinescence is probably the most important factor contributing to slowing down the bite rate. However, for most spiny species, spinescence alone is not sufficient to provide efficient protection: the best protection can be achieved only by species such as *Z. mucronata* or *A. nilotica* having both spines and a high number of axis categories contributing to the cage. The costs related to setting up structural defences are probably really high for these species. However, we expect these to be compensated by reduced herbivory, as these plants offer only very slow foraging rates to the herbivore (Fig. 4).

The cage effect revealed here suggests that the juvenile phase of cagy plants should be a particularly vulnerable life stage. To reach a 'safe' life stage, these plants should not only produce spines, but a 3D architecture composed of all the axis categories, that is, set up their whole architectural unit (Barthélémy & Caraglio 2007). Architectural analysis on species in environments not subject to intense herbivory show that the completion of the architectural unit is frequently achieved after a long time: for example after 7 years for *Rhamnus cathartica* and 13 years for *Cornus sericea* (Charles-Dominique, Edelin & Bouchard 2010; Charles-Dominique *et al.* 2012). Remaining unprotected for such a long time would be lethal for tree species exposed to high herbivory pressure. This therefore suggests

that cagy plants should have either an accelerated set up of their architectural units or exceptional resprouting abilities with a stock accumulation phase followed by the rapid development of their architectural unit. Studying the time needed to set up a cage but also the ontogeny changes in caginess after the sapling stage would improve our understanding of the demography of trees where browsing herbivores are abundant.

FUTURE RESEARCH DIRECTIONS

Our study provides strong experimental support to the hypothesis that cagy architecture may help some plant species to survive in a landscape with high herbivory pressure. However, it is clear that some physically unprotected species also persist in these landscapes, although possibly at lower abundance. This remains to be investigated. It is however well-known that some structurally unprotected species could compensate by being protected chemically by toxins or digestibility reducing compounds (Hanley & Lamont 2002; Wilson & Kerley 2003; Hanley *et al.* 2007; Sebata & Ndlovu 2010). However, this trade-off between physical and chemical defences against mammalian herbivores has until now be focused on spines as the only physical defences (Hanley *et al.* 2007; Shipley 2007). We have shown here that whole-tree structure affect herbivore foraging, and that it should be accounted for when assessing the plant's ISDs. This opens new avenues to better understand the evolution of plant defences and physical/chemical defences trade-offs, in savannas and elsewhere. In this study, we focussed on the branching properties which would be stable at the species level. Trees also display a wide range of responses to browsing, including resprouting, that could affect caginess. A great step forward in understanding the cage architecture would be to assess the contribution of developmental properties allowing for these responses, such as for example the presence of accessory buds, the viability of lateral buds over extended periods or the ability of short shoots to dedifferentiate into a long shoot (Barthélémy & Caraglio 2007). Finally, further studies are needed to define which size ranges of browsers are affected by tree cage architecture.

Authors' contributions

T.C.-D. and S.C.-J. conceived the project; T.C.-D., J.-F.B., E.L.R. and S.C.-J. designed the methodology; T.C.-D., J.-F.B., E.L.R. collected the data; T.C.-D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank William J. Bond, Peter Scogings and Norman Owen-Smith for their insights regarding plant–herbivore interactions and comments on the experimental design and Peter Scogings, Francois du Toit, Jabulani Memela, the Owen Sithole College of Agriculture and HiP Research Centre for their logistical support and help they provided. We would also like to thank SAVARID Project (ANR-11-CEPL-003-06) for support funding. Ethical approval for this project was given by the Science Animal Ethics Committee of the University of Cape Town [protocol number 2014/V8/TCD].

Data accessibility

All data used in this manuscript are present in the manuscript and its supporting information.

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Received 2 August 2016; accepted 23 March 2017

Handling Editor: Clare McArthur

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Drawing of saplings for the 11 species.

Fig. S2. Experimental setup and tree species before and after browsing.

Table S1. Architectural properties and investment in structural defence for the 11 tree species.

Table S2. Goat bite rates on isolated branches and inside the crown for 11 plant species.

Table S3. Dataset – Goat bite rate measurements (measured over 10 bites) on isolated branches and inside the crown for 11 plant species.