

# Plant defence traits among discrete vegetation assemblages in a mesic savanna landscape in Kenya

## Research Article

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### Abstract

A trade-off between structural and chemical defences against herbivory in woody plants is alleged to depend on edaphic factors in African savannas. We studied anti-herbivory traits, in an edaphic mosaic of fertile and infertile soils within a savanna landscape in East Africa, towards elucidating herbivory defence traits expressions in woody plants of African savannas. We used data of 81 plants for 8 species from 8 sites — four sites from fertile soils (42 plants) and another four sites from infertile soils (39 plants). We did not find a general divide between structural and chemical strategies in our data. Instead, we found a range of defence traits combinations. Our results highlight that in woody plants of African savannas, chemical and structural defences can augment each other, and not necessarily trade-off. The diversity of herbivores, ranging from insects to mesobrowsers, may have driven the evolution of multiple defence strategies within the African savannas.

## Introduction

Plants are primary producers in most ecosystems (Woodwell and Whittaker 1968). It is therefore not surprising that one of the most prominent sets of adaptations in their life history is defence against natural enemies. Essentially, plants employ several different lines of defence strategies against herbivory, including structural (Hanley *et al.* 2007, War *et al.* 2018) and chemical (War *et al.* 2018) ones. Structural defence traits, such as leaf pubescence and leaf sclerophylly, affect herbivores by decreasing both palatability and digestibility (Hanley *et al.* 2007). Spinescence, another form of structural defence trait where parts of the plant shoot are modified into sharp tips, also affects herbivory by reducing feeding rates (Gowda 1996). Among the chemical defence types, tannins serve as a potent defensive secondary metabolite, as they bind proteins, inhibit enzymatic activity, and render protein present in a food nutritionally unavailable for herbivory (Mazid *et al.* 2011, Swain 1977).

Until present, a trade-off between structural and chemical defences is alleged for fertile soil fine-leaved and infertile soil broad-leaved African savannas woody plants (Scholes and Walker, 2004). The basis for this hypothesised dichotomy is that African savannas fine-leaved woody plants, growing in nutrient-rich areas, tend to have high nutrient content leaves that are attractive to herbivores. As such, for the trees to defend themselves from intense herbivores browsing, they invest in structural defence strategy. Broad-leaved trees growing in nutrient-poor areas in African savanna landscapes, on the other hand, are purported to employ a chemical defence strategy (e.g., low leaf nutrient content and high secondary metabolites), which makes them unattractive to herbivores. Strong empirical support for a trade-off between the two defences (structural and chemical) in plants is however weakly reported in the field (see Moles *et al.* 2013).

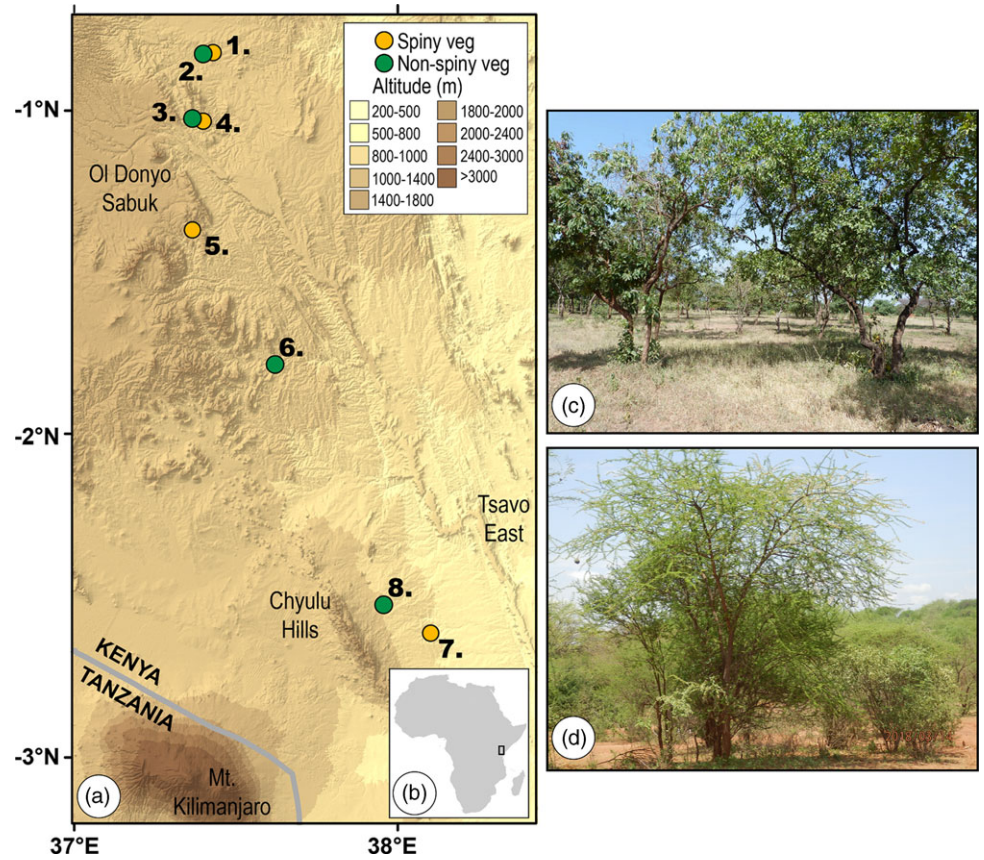
In this study, using nutrient-rich and nutrient-poor soils common trees from a savanna landscape in Kenya, we further understanding of anti-herbivore traits dynamics in woody trees of African savannas. We test a support for the chemical and structural defences trade-off hypothesis in nutrient-rich versus -poor soils African savanna wood plants.

## Materials and Methods

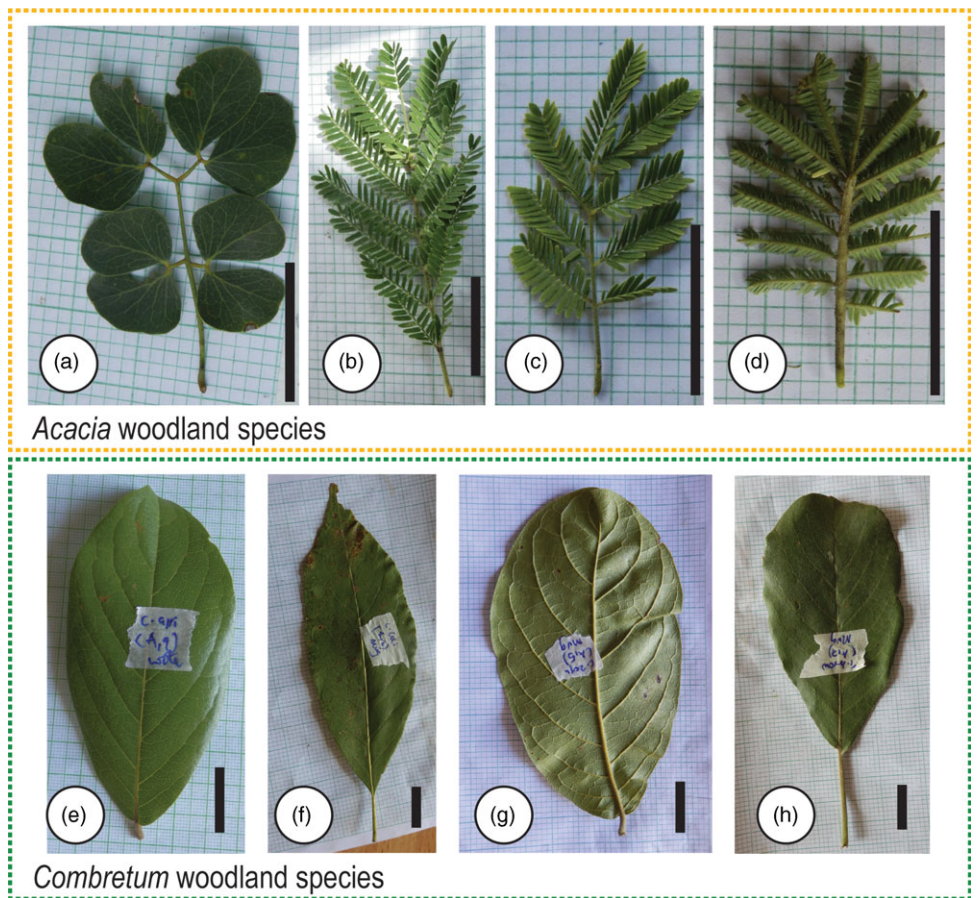
### Description of study sites

The study was conducted at southeastern part of Kenya (0.67°S to 2.62°S, 37.70E° to 38.09E°; Figure 1a), in East Africa (Figure 1b). Study sites comprise a set of four sites from broad-leaved

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**Figure 1.** Sampling sites and exemplar of vegetation types. (a) Location of fertile soil fine-leaved (circle, orange) and infertile broad-leaved (triangle, green) vegetation types, (b) position of study area in tropical Africa, (c) broad-leaved *Combretum* dominated woodlands, and (d) fine-leaved *Acacia* dominated woodlands.



**Figure 2.** (a–h) Representative leaf specimens of fertile soil *Acacia* woodland species (a) *Acacia mellifera*, (b) *A. nilotica*, (c) *A. senegal*, and (d) *A. tortilis*. (e–h) Representative leaf specimens of infertile soil *Combretum* woodland species (e) *Combretum apiculatum*, (f) *C. collinum*, (g) *C. zeyheri*, and (h) *Terminalia brownii*.



woody plant communities (Figure 1c), and another set of four sites from fine-leaved woody plant communities (Figure 1d). In the area, fine- and broad-leaved woody plant communities grow in relatively nutrient rich and nutrient poor soils, respectively (see Kimeu *et al.* 2020). Domestic herds (largely goats) and small African mammalian browsers (e.g., dik-diks and antelopes) are the browsing ungulates predominant in the study vegetation. However, the vegetation is part of the larger East African savannas, which in the past formed one continuous ecosystem that harboured a large population of African mega-herbivores (Marchant *et al.* 2018). The study vegetation is thus likely evolved in the presence of large densities of mega-herbivores, and perhaps under influence of fire — the other major disturbance to the vegetation in African savanna landscapes (see Bond 2008, Sankaran *et al.* 2008 and also Midgley *et al.* 2015).

### Sampling strategy

We sampled woody plant species from eight sites — four sites from fertile soil fine-leaved *Acacia* dominated vegetation and another four sites from infertile soil broad-leaved *Combretum* dominated vegetation — for leaf samples. Sampling was conducted within a 2-week period in December 2019 to January 2020. Fully expanded mature leaves were sampled from three mature individuals (10 leaves per individual) of each study species at every site the species occurred. Only indigenous and the commonest woody species were sampled, and these include spiny *Acacia* and non-spiny Combretaceae species, which had previously showed to be the most dominant and frequent species to the study area (Kimeu *et al.* 2020).

### Plant traits measurement

Four leaf traits including specific leaf area (SLA), nitrogen (N), carbon (C), and condensed tannins (CTs) were measured. SLA index for every sample plant was calculated from averaged leaf areas and masses taken from a set of 10 mature and undamaged leaves collected per individual sample plant. Areas for the leaf samples were determined using the open-source software ImageJ (Abramoff *et al.* 2004); and images used in the ImageJ encompassed a photograph of a whole leaf (i.e., including both petiole and rachis) photographed shortly after its collection (see Figure 2). The leaf weights were measured on air-dried leaf samples using a 0.01 gram digital electronic portable measuring scale. Leaf weighing was carried out at the University of Cape Town in the Biological Science department ecology laboratory.

Measurement of leaf chemical traits used the same leaf samples examined for SLA. Specifically, the 10 leaves collected for each individual plant sample were pooled into one composite sample. Each composite was then mill ground to pass through a 2-mm sieve using a Hammer mill (United Scientific, Cape Town, USA). Leaf nitrogen (N) and carbon (C) contents were analysed using Thermo Scientific FLASH 2000 CHN Elemental Analyser (Thermo Fisher Scientific Inc., Massachusetts, USA). We used the protocol by Porter *et al.* (1986), as modified by Hagerman (2002), for quantifying CTs in plant samples leaves, and used purified *Sorghum* tannin as the protocol calibration standard (Hattas and Julkunen-Tiitto 2012).

### Statistical analyses

To assess how well the predicted groups (nutrient-rich soils fine- and nutrient-poor soils broad-leaved woody plants) were able to assign each sample species to the correct group based on the

**Table 1.** Commonest woody plant species in fertile soil fine-leaved and infertile soil broad-leaved plant communities at the mesic savanna of southeastern Kenya

Vegetation community	Species	Sampled individuals
Fine-leaved	<i>Acacia mellifera</i> (M.Vahl) Benth.	12
	<i>A. nilotica</i> (L.) Willd.	9
	<i>A. senegal</i> (L.) Willd.	9
	<i>A. tortilis</i> (Forssk.) Hayne	12
Broad-leaved	<i>Combretum apiculatum</i> Sond.	9
	<i>C. collinum</i> Fresen	12
	<i>C. zeyheri</i> Sond.	9
	<i>Terminalia brownii</i> Fresen	9

**Table 2.** Coefficient of linear discriminants for the study leaf traits along axes LD1 and 2 derived from the study linear discriminant model.

Leaf traits	Coefficient of linear discriminants	
	LD1	LD2
Specific leaf area (SLA)	−0.55558	0.150028
Nitrogen (N)	−2.69444	−0.45165
Carbon (C)	0.360062	0.447298
Condensed tannins (CTs)	0.237265	−3.10071

sampled leaf traits (SLA, nitrogen, carbon, and CTs), we ran linear discriminant analysis (LDA) using the ‘Mass’ package in R. Further, we used the boxplot tool (in the R ‘stats’ package) to evaluate spread of values for the sampled leaf traits across the sample species. To test evidence for a trade-off in allocation to leaf traits associated with structural defence versus chemical defence for nutrient-rich soils, fine-leaved and nutrient-poor soils, broad-leaved woody species, we correlated SLA (which encompasses a plant’s sclerophylly index aspect) against each of the three sampled leaf chemical traits (nitrogen, carbon, and CTs). We used the ‘cor.test’ function of the R ‘stats’ package, and we plotted the plants for the groups in scatterplots spaces, with different symbols used for each group.

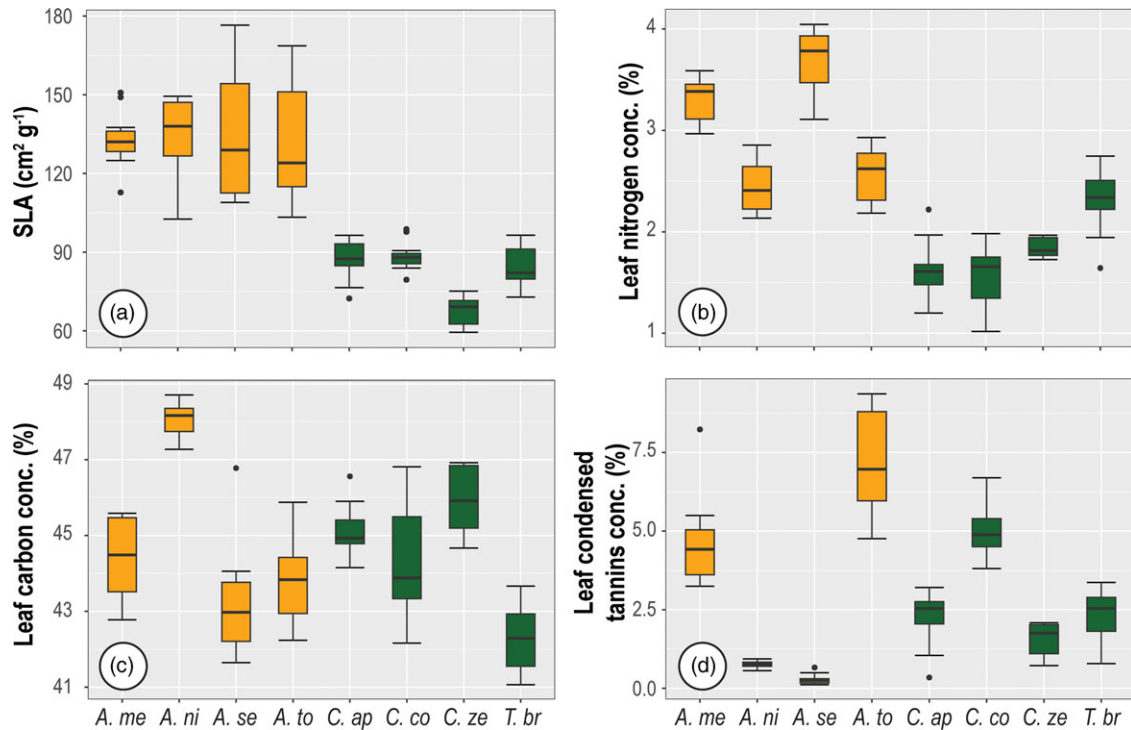
### Results

A total of 81 plants (42 and 39 of from sites of *Acacia* dominated and *Combretum* dominated woody plant communities, respectively) were recorded for this study (Table 1 and Appendix 1).

### Defences between fine-leaved and broad-leaved woody plant communities

LDA revealed 86.98% of variance of the studied leaf traits distributed along LDA1 (50.45%) and LD2 (36.53%). Fine-leaved, spinescent *Acacia* and broad-leaved, non-spinescent Combretaceae species loading along axis LDI were principally correlated with SLA and nitrogen, and along LD2 with carbon and CTs (Table 2).

When we compared measurements for each of the four sampled leaf traits between fine-leaved and broad-leaved plant functional groups, both SLA and leaf nitrogen differed markedly between the two



**Figure 3.** Boxplots showing SLA, leaf nitrogen, total carbon, and condensed tannin traits profiles for the common species (*Acacia mellifera* (A.me), *A. nilotica* (A.ni), *A. senegal* (A.se), *A. tortilis* (A.to), *Combretum apiculatum* (C.ap), *C. collinum* (C.co), *C. zehyeri* (C.ze), and *Terminalia brownii* (T.br)) of spiny, fine-leaved (orange) and non-spiny, broad-leaved (green) vegetation systems of the mesic savannas of southeastern Kenya.

plant groups. All fine-leaved spiny *Acacia* species had higher SLA than broad-leaved non-spiny Combretaceae species (Figure 3a). Fine-leaved spiny *Acacia* species again had generally higher leaf nitrogen content than Combretaceae species (Figure 3b). This pattern however was not repeated for leaf carbon and CTs — that is, both traits (carbon and CTs) had high and low peaks, which were species-specific rather than vegetation-type-specific (Figure 3c and d).

#### Defence strategies trade-offs between fine- and broad-leaved woody plant communities

Despite some overlap, the current data revealed evidence for a trade-off of leaf nitrogen content profiles between *Acacia* and Combretaceae species (Figure 4a). The correlation coefficient for leaf nitrogen, between fine- and broad-leaved vegetation leaf categories, is significant ( $r = 0.67$ ,  $p < 0.001$ ). Carbon and CTs, however, did not show evidence of a trade-off between fine- and broad-leaved leaf samples, where the correlation coefficients recovered for carbon and CTs between fine- and broad-leaved vegetation leaf categories both are low and not significant ( $r = 0.12$ ,  $p = 0.240$  for carbon (Figure 4b), and  $r = 0.13$ ,  $p = 0.210$  for CTs (Figure 4c).

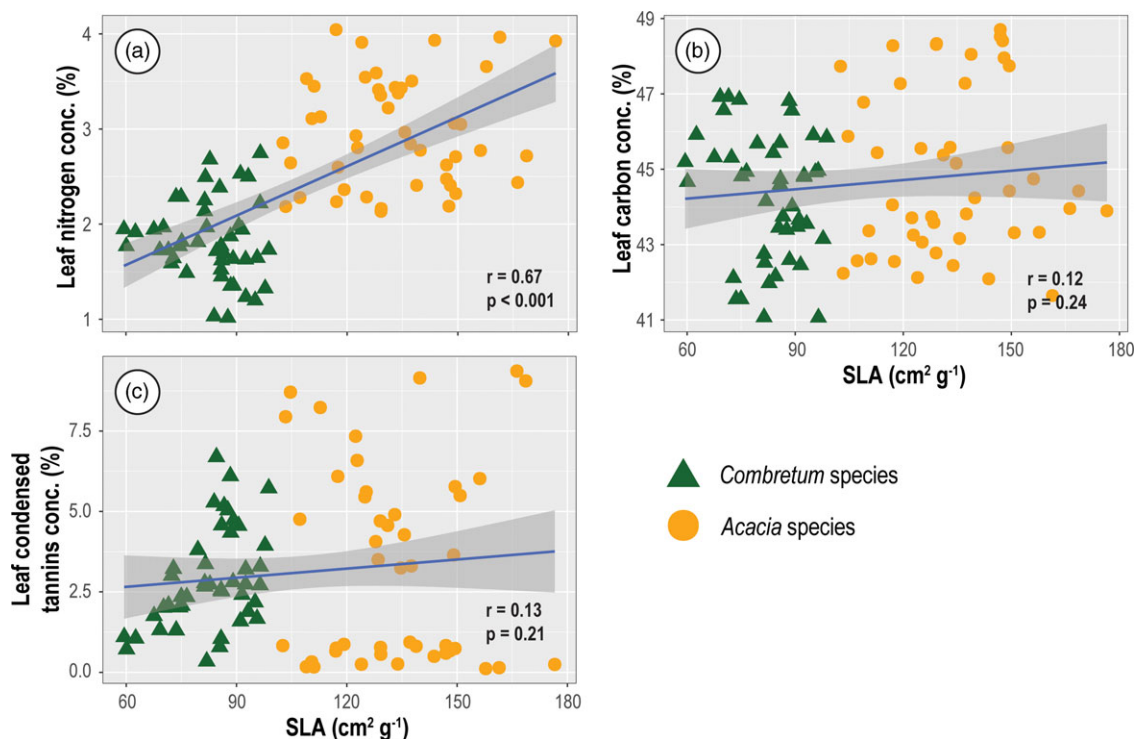
#### Discussion

This study set to test a trade-off between structural and chemical defence strategies alleged for fertile soil fine-leaved and infertile soil broad-leaved African savanna woody plants (Scholes and Walker 2004). The data presented here did not consistently support a trade-off between structural and chemical defence strategies in fertile soil fine-leaved and infertile soil broad-leaved woody plant samples. For example, results from the LDA showed that SLA and leaf nitrogen

contributed the most to the first axis, while carbon and CTs contributed the most to the second axis, suggesting that there is no trade-off between the two traits sets in the studied vegetation systems. Had there been evidence for a strong trade-off between them, they would be expected to separate along a single axis. Furthermore, both leaf SLA and N indices were generally different between fertile soil fine-leaved and infertile soil broad-leaved plant samples, with a trend of higher quality (i.e., higher SLA and N) in fertile soil fine-leaved plant samples compared to the infertile soil broad-leaved plant samples). This trend however is not replicated for the other sampled two leaf traits (leaf carbon [C] and CTs).

The concept that chemical and structural defence syndromes can augment each other and do not necessarily trade-off has emanated from this work. This pattern is curious given that a previous work by Tomlinson *et al.* (2016) reported a support for the Scholes and Walker (2004) chemical and structural defences trade-off hypothesis in nutrient-rich versus -poor soils African savanna wood plants — although also there are other data that show in African savanna landscapes a section of spiny woody species growing in nutrient-rich soils could invest in chemical anti-herbivore defences equally to non-spiny broad-leaved plants growing in nutrient-poor soils (Wigley *et al.* 2018, 2019). The current data perhaps is highlighting Agrawal (2011) intuition that a simple trade-off model is unlikely as multiple defence traits in concert would be more effective, that is, a diverse suite of herbivores with different responses to specific chemicals or defences may attack a particular species.

In the simple trade-off model, fine-leaved species should not invest in high-carbon concentration (Figure 3c), when fine-leaved species are assumed to be defended by structural defences rather chemical defences (Scholes and Walker 2004) — although carbon is also a critical structural element that provide



**Figure 4.** Pearson correlations of SLA plotted against leaf chemical traits nitrogen, carbon, and condensed tannins for spiny fine-leaved and non-spiny broad-leaved vegetation species of the mesic savanna of southeastern Kenya.

biomechanical support for plant tissues (Niinemets and Tamm, 2005). It is also not clear why some fine-leaved species invest in high CTs (Figure 3d), and yet this is a trait expected in broad-leaved savanna trees in the simple trade-off model (see Scholes and Walker, 2004, and also Tomlinson *et al.*, 2016). CT concentration has been shown to influence herbivores' diet choice as it makes nutrients less available after ingesting (Ward and Young 2002, Scogings *et al.* 2004). Nonetheless, similar to our results, both low and high CTs indices have been previously reported by other studies focusing on fine-leaved spiny woody plant species in African savannas. In north-central Kenya, fine-leaved *Acacia drepanolobium* browsed by antelope and mega-herbivores contained 1.0 to 17.1% CTs (Ward and Young 2002). Furthermore, in the same study area, *A. etbaica* and *A. brevispica* contained 1.3% and 20.8% CTs, respectively (Ford *et al.* 2014; Ward and Young 2002).

Aspects of phylogenetic history are known to shape expression of suites of defence traits in species, and especially when species are closely related (Agrawal and Fishbein 2006). In the current study, for each vegetation type we sampled species from a singular family (Fabaceae and Combretaceae for fine- and broad-leaved vegetation types, respectively). While we take seriously the recognizant of a consequence of functional attributes having deep historical origins, we argue that the trait patterns recovered in our data cannot all be explained by biases due to phylogenetic signals. In the study area, for example, there are two Combretaceae species (*Combretum aculeatum* and *Terminalia spinosa*, see Kimeu *et al.* 2020) with relatively fine-leaved and spines, but none of the sampled Combretaceae species here has these traits.

Overall, this study results have shown that plant anti-herbivory defences are complex, and perhaps operating in tandem. The dominant species in each vegetation type in the study showed

the two defence strategies may overlap, for example, at least with some species combining structural defence strategy traits (nutritious leaves [high SLA and nitrogen]) with chemical defences (CTs and carbon). The results affirm the logical thought that it is inappropriate to follow a single line of defence in plants as plants themselves can employ multiple sets of defences (see Agrawal and Fishbein 2006). Lastly and more importantly, our study greatly contributes to understanding plants' herbivory niche partition that could account for the high herbivore diversity supported by wood species within landscapes of East Africa savannas (Appendix 1).

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**Competing interest.** The authors have declared that no competing interests exist, given that this study was not research commissioned by industry.

**Publishing Ethics.** This data and work are not plagiarised. However, the work is based on a chapter submitted towards a PhD by the first author of this article and with a permission from the other authors

**Ethical statement.** None.

## References

- Abramoff MD, Magalhães PJ and Ram SJ (2004) Image processing with ImageJ. *Biophotonics International* 11, 36–42.
- Agrawal AA (2011) Current trends in the evolutionary ecology of plant defence. *Functional Ecology* 25, 420–432.

- Agrawal AA and Fishbein M** (2006) Plant defense syndromes. *Ecology* **87**, 132–149.
- Bond WJ** (2008) What limits trees in C4 grasslands and savannas? *Annual Review* **39**, 641–659.
- Ford AT, Goheen JR, Otieno TO, Bidner L, Isbell LA, Palmer TM, Ward D, Woodroffe R and Pringle RM** (2014) Large carnivores make savanna tree communities less thorny. *Science* **346**, 346–349.
- Gowda JH** (1996) Spines of *Acacia tortilis*: what do they defend and how. *Oikos* **77**, 000–000.
- Hagerman AE** (2002) The tannin handbook. Available at: <http://www.users.muohio.edu/hagermae>.
- Hanley ME, Lamont, BB, Fairbanks, MM and Rafferty CM** (2007) Plant structural traits and their role in anti-herbivore defense. *Perspectives in Plant Ecology, Evolution and Systematics* **8**, 157–178.
- Hattas D and Julkunen-Tiitto R** (2012) The quantification of condensed tannins in African savanna tree species. *Phytochemistry Letters* **5**, 329–334.
- Kimeu JM, Mwachala G, Reichgelt T and Muasya AM** (2020) Characterization of alternative stable vegetation assemblages in a mesic savanna in Kenya. *African Journal of Ecology* **00**, 1–11.
- Marchant R, Richer S, Boles O, Capitani C, Courtney-Mustaphi GJ, Lane P and Wright D** (2018) Drivers and trajectories of land cover change in East Africa: human and environmental interactions from 6000 years ago to present. *Earth-Science Reviews* **178**, 322–378.
- Mazid M, Khan TA and Mohammad F** (2011) Role of secondary metabolites in defense mechanisms of plants. *Biology and Medicine* **3**, 232–249.
- Midgley JJ, Sawe T, Abanyam P, Hintsa, K and Gacheru P** (2015) Spinescent East African savannah acacias also have thick bark, suggesting they evolved under both an intense fire and herbivory regime. *African Journal of Ecology* **54**, 118–120.
- Moles AT, Peco B, Wallis IR et al.** (2013) Correlations between physical and chemical defences in plants: tradeoffs, syndromes, or just many different ways to skin a herbivorous cat? *New Phytologist* **198**, 252–263.
- Niinemetts Ü and Tamm Ü** (2005) Species differences in timing of leaf fall and foliage chemistry modify nutrient resorption efficiency in deciduous temperate forest stands. *Tree Physiology* **25**, 1001–1014.
- Porter LJ, Hrstich LN and Chan BC** (1986) The conversion of procyanidins and prodelphinins to cyanidin and delphinin. *Phytochemistry* **25**, 223–230.
- Sankaran M, Ratnam J and Hanan NP** (2008) Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* **17**, 236–245.
- Scholes RJ and Walker BH** (2004) *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge: Cambridge University Press.
- Scogings P, Dziba E and Gordon IJ** (2004) Leaf chemistry of woody plants in relation to season, canopy retention and goat browsing in a semi-arid subtropical savanna. *Austral Ecology* **29**, 278–286.
- Swain T** (1977) Secondary compounds as protective agents. *Annual Review of Plant Physiology* **28**, 479–501.
- Tomlinson KW, van Langevelde F, Ward D, Prins HHT, de Bie S, Vosman B, Sampaio EVSB and Sterck FJ** (2016) Defence against vertebrate herbivores trades off into architectural and low nutrient strategies amongst savanna Fabaceae species. *Ikos* **000**, 001–011.
- War AR, Taggar GK, Hussain B, Taggar MS, Nair RM, Sharma HC** (2018) Plant defence against herbivory and insect adaptations. *AoB PLANTS* **10**, ply037.
- Ward D and Young TP** (2002) Effects of large mammalian herbivores and ant symbionts on condensed tannins of *Acacia drepanolobium* in Kenya. *Journal of Chemical Ecology* **28**, 921–937.
- Wigley BJ, Coetsee C, Augustine DJ, Ratnam J, Hattas D and Sankaran M** (2019) A thorny issue: Woody plant defense and growth in an East African savanna. *Journal of Ecology* **107**, 1839–1851.
- Wigley BJ, Fritz H and Coetsee C** (2018) Defence strategies in African savanna trees. *Oecologia* **187**, 797–809.
- Woodwell GM and Whittaker RH** (1968) Primary production in terrestrial ecosystems. *American Zoologist* **8**, 19–30.

## Appendix 1

List of woody plants for the Acacia and Combretum plant communities' common species alongside their respective four leaf traits

Species	Study site	SLA (cm <sup>2</sup> g <sup>-1</sup> )	N%	C%	CTs%
<i>A.mellifera</i>	Acacia WL1	129.101	3.354	42.779	4.704
<i>A.mellifera</i>	Acacia WL1	112.774	3.129	45.441	5.229
<i>A.mellifera</i>	Acacia WL1	131.122	3.222	45.378	4.565
<i>A.mellifera</i>	Acacia WL4	128.514	3.414	43.586	3.502
<i>A.mellifera</i>	Acacia WL4	135.644	2.967	43.163	4.275
<i>A.mellifera</i>	Acacia WL4	124.917	3.545	45.554	5.452
<i>A.mellifera</i>	Acacia WL5	134.680	3.431	45.158	3.242
<i>A.mellifera</i>	Acacia WL5	127.862	3.589	43.74	4.062
<i>A.mellifera</i>	Acacia WL5	150.819	3.05	43.316	5.492
<i>A.mellifera</i>	Acacia WL7	133.033	3.438	45.585	4.901
<i>A.mellifera</i>	Acacia WL7	149.052	3.060	45.576	3.645
<i>A.mellifera</i>	Acacia WL7	137.524	3.505	43.816	3.304
<i>A.nilotica</i>	Acacia WL1	146.948	2.622	48.708	0.936
<i>A.nilotica</i>	Acacia WL1	129.246	2.164	48.336	0.810
<i>A.nilotica</i>	Acacia WL1	138.843	2.407	48.051	0.559
<i>A.nilotica</i>	Acacia WL4	137.163	2.843	47.282	0.832
<i>A.nilotica</i>	Acacia WL4	146.948	2.474	48.523	0.829
<i>A.nilotica</i>	Acacia WL4	129.173	2.134	48.312	0.666
<i>A.nilotica</i>	Acacia WL5	147.997	2.408	47.958	0.773
<i>A.nilotica</i>	Acacia WL5	102.588	2.854	47.734	0.594
<i>A.nilotica</i>	Acacia WL5	117.117	2.235	48.281	0.741
<i>A.senegal</i>	Acacia WL1	176.535	3.925	43.898	0.173
<i>A.senegal</i>	Acacia WL1	123.972	3.910	42.126	0.250
<i>A.senegal</i>	Acacia WL1	108.986	3.529	42.778	0.244
<i>A.senegal</i>	Acacia WL4	110.449	3.109	43.367	0.660
<i>A.senegal</i>	Acacia WL4	157.772	3.656	43.328	0.142
<i>A.senegal</i>	Acacia WL4	161.418	3.966	41.648	0.115
<i>A.senegal</i>	Acacia WL5	117.000	4.044	44.056	0.323
<i>A.senegal</i>	Acacia WL5	111.057	3.450	42.622	0.166
<i>A.senegal</i>	Acacia WL5	143.735	3.933	42.092	0.497
<i>A.tortilis</i>	Acacia WL1	104.671	2.643	45.876	6.089
<i>A.tortilis</i>	Acacia WL1	156.167	2.774	44.743	5.607
<i>A.tortilis</i>	Acacia WL1	125.268	2.285	43.065	6.021
<i>A.tortilis</i>	Acacia WL4	117.543	2.597	42.551	8.708
<i>A.tortilis</i>	Acacia WL4	166.242	2.438	43.957	7.337
<i>A.tortilis</i>	Acacia WL4	168.665	2.278	42.571	9.057
<i>A.tortilis</i>	Acacia WL5	107.221	2.930	43.71	9.362
<i>A.tortilis</i>	Acacia WL5	122.391	2.321	44.424	5.395
<i>A.tortilis</i>	Acacia WL5	149.453	2.777	44.242	9.149
<i>A.tortilis</i>	Acacia WL7	139.842	2.184	42.239	5.771
<i>A.tortilis</i>	Acacia WL7	103.346	2.803	43.256	9.903

(Continued)



(Continued)

Species	Study site	SLA (cm <sup>2</sup> g <sup>-1</sup> )	N%	C%	CTs%
<i>A.tortilis</i>	Acacia WL7	122.811	3.602	43.260	9.879
<i>C.apiculatum</i>	Combretum WL2	85.800	2.587	45.308	1.045
<i>C.apiculatum</i>	Combretum WL2	72.348	2.488	44.930	4.007
<i>C.apiculatum</i>	Combretum WL2	76.483	1.968	44.154	2.343
<i>C.apiculatum</i>	Combretum WL3	81.904	2.198	45.903	2.738
<i>C.apiculatum</i>	Combretum WL3	92.472	2.451	44.742	2.176
<i>C.apiculatum</i>	Combretum WL3	95.055	2.645	44.921	3.204
<i>C.apiculatum</i>	Combretum WL6	85.916	2.635	46.560	1.666
<i>C.apiculatum</i>	Combretum WL6	92.505	2.523	44.595	2.807
<i>C.apiculatum</i>	Combretum WL6	95.604	2.219	44.962	0.558
<i>C.collinum</i>	Combretum WL2	83.925	2.030	40.433	4.555
<i>C.collinum</i>	Combretum WL2	79.501	1.812	40.684	5.868
<i>C.collinum</i>	Combretum WL2	97.763	2.324	43.151	4.209
<i>C.collinum</i>	Combretum WL3	98.773	1.731	40.845	5.283
<i>C.collinum</i>	Combretum WL3	88.333	1.873	40.814	2.806
<i>C.collinum</i>	Combretum WL3	87.653	2.017	40.394	3.943
<i>C.collinum</i>	Combretum WL6	89.178	2.354	44.016	5.723
<i>C.collinum</i>	Combretum WL6	85.965	1.619	41.559	6.101
<i>C.collinum</i>	Combretum WL6	84.545	1.717	42.16	5.037
<i>C.collinum</i>	Combretum WL8	90.595	1.982	40.472	4.729
<i>C.collinum</i>	Combretum WL8	88.439	2.352	41.594	4.572
<i>C.collinum</i>	Combretum WL8	86.643	1.689	41.749	6.691
<i>C.zeyheri</i>	Combretum WL2	60.105	1.768	44.667	0.718
<i>C.zeyheri</i>	Combretum WL2	75.142	2.814	44.817	3.074
<i>C.zeyheri</i>	Combretum WL2	59.470	1.946	45.195	1.101
<i>C.zeyheri</i>	Combretum WL3	71.524	2.725	46.921	2.083
<i>C.zeyheri</i>	Combretum WL3	62.587	1.905	45.413	1.055
<i>C.zeyheri</i>	Combretum WL3	69.175	2.667	46.573	2.315
<i>C.zeyheri</i>	Combretum WL6	74.524	2.627	47.271	1.251
<i>C.zeyheri</i>	Combretum WL6	67.587	1.971	45.317	1.937
<i>C.zeyheri</i>	Combretum WL6	70.175	2.767	45.476	2.407
<i>T.brownii</i>	Combretum WL2	72.858	2.386	43.451	2.349
<i>T.brownii</i>	Combretum WL2	74.981	2.494	40.52	1.786
<i>T.brownii</i>	Combretum WL2	91.512	1.943	42.458	2.413
<i>T.brownii</i>	Combretum WL3	85.443	2.288	41.553	3.367
<i>T.brownii</i>	Combretum WL3	81.549	2.249	40.072	1.308
<i>T.brownii</i>	Combretum WL3	73.606	2.500	43.554	2.669
<i>T.brownii</i>	Combretum WL6	81.367	1.942	42.458	3.290
<i>T.brownii</i>	Combretum WL6	93.189	2.136	40.755	1.413
<i>T.brownii</i>	Combretum WL6	96.455	2.530	43.666	2.775

SLA, specific leaf area; N, nitrogen content; C, carbon content; and CTs, condensed tannins used for investigations of the trade-off between structural and chemical defences against herbivory phenomenon in African savanna woody plants.