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1 **Secondary metabolites and nutrients of woody plants in relation to**  
2 **browsing intensity in African savannas**

3

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20

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25

26 **Abstract** Carbon-based secondary metabolites (CBSMs) are assumed to function as  
27 defences that contribute to herbivore-avoidance strategies of woody plants. Severe  
28 browsing has been reported to reduce concentrations of CBSMs and increase N  
29 concentrations in individual plants, causing heavily browsed plants to be characterised  
30 by N-rich/C-poor tissues. We hypothesised that concentrations of condensed tannins  
31 (CT) and total polyphenols (TP) should decrease, or N increase, in relation to  
32 increasing intensity of browsing, rendering severely browsed plants potentially more  
33 palatable (increased N:CT) and less N-limited (increased N:P) than lightly browsed  
34 ones. We sampled naturally browsed trees (taller than 2 m) of four abundant species  
35 in southern Kruger National Park, South Africa. Species-specific relationships  
36 between N:CT, CT, TP and P concentrations and increasing browsing intensity were  
37 detected, but N and N:P were consistently invariable. We developed a conceptual  
38 post-hoc model to explain diverse species-specific CBSM responses on the basis of  
39 relative allocation of C to total C-based defence traits (e.g., spines/thorns,  
40 tough/evergreen leaves, phenolic compounds). The model suggests that species with  
41 low allocation of C to C-based defence traits become C-limited (potentially more  
42 palatable) at higher browsing intensity than species with high allocation of C to C-  
43 based defences. The model also suggests that when N availability is high, plants  
44 become C-limited at higher browsing intensity than when N availability is low.

45

46 **Key words** Functional trait, Growth-defence, Herbivore, Photosynthesis, Source:sink

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51 **Introduction**

52

53 Carbon-based secondary metabolites (CBSMs), such as tannins, are assumed to  
54 function as chemical defences that contribute to the herbivore-avoidance strategies of  
55 woody plants (Skarpe and Hester 2008). While defoliation may induce defences in  
56 woody plants (Ward and Young 2002; Wessels et al. 2007), severe browsing has been  
57 reported to have the opposite effect, by causing either increased N concentrations or  
58 reduced tannin concentrations in individual plants (du Toit et al. 1990; Danell et al.  
59 2003; Persson et al. 2005). Therefore, heavily browsed plants may switch to a  
60 vegetative state characterised by N-rich/C-poor tissues. The switch puts the plant in a  
61 positive feedback loop because it potentially increases a plant's risk of being browsed  
62 again (Fornara and du Toit 2007; Skarpe and Hester 2008). The phenomenon has been  
63 compared to grazing lawns in the Serengeti and the term "browsing lawn" has been  
64 used to describe it (McNaughton 1984; Fornara and du Toit 2007). One explanation  
65 given for positive feedback in savanna trees is preferential allocation of C to growth  
66 of new shoots rather than C-based chemical defences (Fornara and du Toit 2007;  
67 Hrabar et al. 2009), which can be achieved when the root:shoot ratio is altered such  
68 that shoot growth increases (Herms and Mattson 1992; Renton et al. 2007). A  
69 simultaneous increase in nutrients may occur to meet the demands of increased  
70 growth (Herms and Mattson 1992; Ågren 2008).

71 A critical component of current research efforts in savannas concerns the  
72 effects of large herbivores on woody plants, with the ultimate objective of developing  
73 improved management policies (O'Keefe and Alard 2002). Understanding how  
74 vegetation responds to management depends on understanding how individual plants  
75 respond to herbivores (Hester et al. 2006; Hobbs 2006). Evidence for the responses of

76 nutrients and CBSMs to browsing intensity is inconsistent among studies in savannas.  
77 Increases in CBSM concentrations, sometimes associated with decreases in [N] and  
78 [P], have been detected in the same season of browsing/clipping or in the growing  
79 season after browsing/clipping (e.g., Bryant et al. 1991; Wessels et al. 2007), but the  
80 reverse pattern, sometimes associated with increased [N] and shoot growth, has also  
81 been detected (e.g., Scogings 1998; Rooke and Bergström 2007). However, no effects  
82 have been detected in numerous cases (e.g., Gowda 1997; Gadd et al. 2001; Katjiua  
83 and Ward 2006; Scogings and Mopipi 2008). Few studies have compared more than  
84 two levels of browsing intensity, which has been inferred from browser abundance or  
85 distance from water.

86         The broad aim of this paper is to explore relationships between browsing  
87 intensity and CBSMs and nutrients in mature leaves of woody species in a semi-arid  
88 savanna. Mature leaves comprise the main component of foliage for most of the  
89 growing season. Because browsing intensity varies among individuals (Skarpe and  
90 Hester 2008), the specific objective was to study the relationships between condensed  
91 tannin (CT), total polyphenol (TP), N and P concentrations and natural variation in  
92 browsing intensity among con-specific individuals under long-term utilisation by  
93 large herbivores. The variation in browsing intensity was not clearly related to any  
94 obvious environmental gradient such as distance from water, altitude, soil type or  
95 texture, or plant density. We assume that the measured chemical traits are responses to  
96 mammal browsing, rather than drivers of browsing, but we also acknowledge that  
97 chemistry may be influential (Scogings et al. 2004; Rooke and Bergström 2007). We  
98 assume that increasing the intensity of browsing increases the root:shoot ratio and  
99 hence the availability of nutrients for growth increases (Scogings and Macanda 2005).  
100 We hypothesise that tannins and phenols decrease (because increased growth

101 demands C), but nutrients (especially N) increase, in relation to increasing intensity of  
102 browsing. From a herbivore's perspective, plants become potentially more palatable,  
103 as reflected by increased N:CT (Palo et al 1993). From a plant's perspective, however,  
104 if increased palatability accompanies a shift in nutritional balance that is detrimental  
105 to the plant, then its fitness is likely compromised. We expected plant nutritional  
106 status to become P-limited relative to N (increased N:P) because P is recycled more  
107 than N (Ågren 2008). We explored the above hypotheses by sampling naturally  
108 browsed trees in Kruger National Park, South Africa, following the "natural  
109 experiment" approach used in other studies (Zinn et al. 2007; Fornara and du Toit  
110 2008). We then conceptualised a functional model to explain diverse responses of  
111 CBSMs among woody species.

112

113

## 114 **Materials and methods**

115

### 116 **Study area**

117

118 The study area comprised 47 ha at Nkuhlu (24° 58' S, 31° 46' E) directly east of the  
119 Sabie River in Kruger National Park, South Africa. Altitude ranges from 200 to 230 m  
120 above mean sea level. The study area included the complete sequence of terrain  
121 morphology from footslope to crest in undulating landscape derived from granite. The  
122 crests and middle slopes were characterized by shallow, sandy, coarse soil overlying  
123 rock and the footslopes below the seepline were characterized by deep, sodic, duplex  
124 soil, which is a typical pattern on catenas in granite-derived, semi-arid landscapes  
125 (Khomo and Rogers 2005, Grant and Scholes 2006). Vegetation on sodic soils is

126 sparse and regarded as more attractive than crest vegetation to large herbivores,  
127 especially grazers and mixed feeders (Tarasoff et al 2007, Levick and Rogers 2008).

128         The climate of the study area is semi-arid subtropical with two broadly distinct  
129 seasons: a hot, occasionally wet, growth season (October–April), and a warm, dry,  
130 non-growing season (Williams et al. 2009). Mean annual rainfall at Skukuza, 30 km  
131 west of Nkuhlu, is ~550 mm. Average daily temperatures at Skukuza are 15.7 °C in  
132 June and 26.6 °C in January. Average minimum temperature in June is 5.7 °C and  
133 average maximum temperature in January is 32.6 °C. Plant communities in the study  
134 area were described by Siebert and Eckhardt (2008). Abundant woody species  
135 (nomenclature follows Schmidt et al. 2007) included *Acacia grandicornuta* and  
136 *Euclea divinorum* on the footslopes, and *Dichrostachys cinerea*, *Acacia exuvialis*,  
137 *Combretum apiculatum* and *Grewia flavescens* on the middle slopes and crests. Most  
138 of the woody species are deciduous and shorter than 10 m. Common mammal  
139 herbivores (nomenclature follows Skinner and Chimimba 2005) included impala  
140 (*Aepyceros melampus*), African elephant (*Loxodonta africana*), hippo (*Hippopotamus*  
141 *amphibius*), black rhino (*Diceros bicornis*), blue wildebeest (*Connochaetes taurinus*),  
142 Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga*), greater kudu  
143 (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), giraffe (*Giraffa*  
144 *camelopardalis*) and scrub hare (*Lepus saxatilis*). Elephant, impala, kudu, giraffe,  
145 black rhino and steenbok include substantial woody vegetation in their diets. Elephant  
146 density in the study area fluctuated, but was estimated to be 0.5-2.0 km<sup>-2</sup>, which is  
147 considered to be high (Grant et al. 2008). A breeding herd of 30-40 impala, several  
148 impala bachelors, two black rhino and an unknown number of steenbok were resident  
149 in the study area, while low numbers of giraffe and kudu were occasionally present.

150

151 Sampling

152

153 The number of plant species used in the study was restricted to four because of  
154 logistical and technical reasons. The species selected were among the most abundant  
155 and evenly distributed in the study area, allowing for the desired sampling strategy to  
156 be implemented (see below). *Acacia grandicornuta* Gerstner is a deciduous legume  
157 with fine, bi-compound leaves and long straight spines in pairs at the nodes.  
158 *Dichrostachys cinerea* (L.) Wright and Arn. subsp. *africana* Brennan and Brummitt  
159 (hereafter referred to as *Dichrostachys cinerea*) is a multi-stemmed, deciduous  
160 legume with fine, bi-compound leaves and stem-spines (short shoots that have sharp  
161 tips). *Combretum apiculatum* Sond. and *Grewia flavescens* Juss. are both deciduous  
162 and broad-leaved, but *C. apiculatum* is a tree, while *G. flavescens* is a many-stemmed  
163 large shrub.

164         Sampling was scheduled according to preliminary observations at the site in  
165 two previous years (Zululand/Sweden Kruger Browse Project – ZSKBP, unpublished  
166 data), which indicated that effects of browsing on CTs and TPs of mature leaves was  
167 most readily detectable in the middle of the wet season (January). Sampling at this  
168 time was appropriate because CTs and TPs are thought to accumulate as the season  
169 progresses (Barton and Koricheva 2010). Our preliminary data also indicated that  
170 sampling in the middle of the wet season was suitable for detecting effects of  
171 browsing on nutrients. Sampling only mature leaves at one time ensured that leaf  
172 phenology would not confound our results. A 30 x 30 m grid was used to randomly  
173 locate 36 sites per soil type. One tree of each study species was sampled in each grid  
174 cell on condition that it was (1) closest to the grid-cell centre, (2) taller than 2 m (1.5  
175 m for *G. flavescens*), and (3) neither obviously stressed by disease, disturbance or



176 neighbours nor obviously growing in a nutrient enriched patch. The minimum height  
177 of selected *G. flavescens* plants was 1.5 m because it seldom grows as tall as 2 m. If  
178 any of the conditions failed to be met for the closest tree, then the next closest tree  
179 that met the conditions was sampled. No tree was sampled if the closest suitable tree  
180 was further than 15 m from the grid-cell centre to avoid infringement of neighbouring  
181 cells.

182         Browsing intensity for each tree was visually estimated as the fraction (%) of  
183 productive canopy volume (including branches bearing leaves or shoots) either below  
184 or above 1.5 m deemed missing because of browsing. The method was subjective, but  
185 all estimates were made by one observer to ensure repeatability. The method was  
186 developed and tested by four observers on four previous occasions including the  
187 observer for the present study. Four types of browsing were observed: (1) leaf  
188 removal by nibbling or stripping, (2) biting of current wet season's shoots, (3) biting  
189 of previous wet seasons' shoots, and (4) accumulated biting of twigs 1-2 years old. It  
190 was presumed that the estimate of accumulated twig-biting mainly represented  
191 browsing within the last two years, and that any older twig-biting was a minor fraction  
192 of the total estimate (Pellew 1983; Oba 1998). Accumulated elephant impact (change  
193 of tree growth form caused by branch or stem breakage) was recorded on a subjective  
194 scale (none, moderate, severe) (Makhabu et al. 2006).

195         Leaf samples were collected from each plant by clipping branches 3-8 mm in  
196 diameter from the northern, sunlit half of the canopy between 1.5 and 2.2 m above  
197 ground, which was within the range of most browsers in the study area. For *G.*  
198 *flavescens*, the lowest permissible height for collection was reduced to 1.0 m because  
199 of its low stature. Branches were collected 1-4 hours after sunrise. Mature (fully  
200 expanded) leaves that did not show signs of severe insect herbivory were removed

201 until a fresh mass of 30-50 g was obtained for drying in an oven for 24 hours at 60 °C.  
202 Dried leaf samples were milled to pass a sieve with 1.0 mm apertures and were  
203 analysed for concentrations of condensed tannins ([CT]) (Porter et al. 1986; Hattas et  
204 al. 2005), total polyphenols ([TP]) (Price and Butler 1977), Kjeldahl-N ([N]) (AOAC  
205 1990) and phosphorus ([P]) (Murphy and Riley 1962). All concentrations were  
206 expressed in mg g<sup>-1</sup> dry mass. [CT] and [TP] were expressed as sorghum tannin  
207 equivalents (STE) and gallic acid equivalents (GAE), respectively. Differences in  
208 concentrations in mature leaves were assumed to reflect differences in absolute  
209 amounts because the limited growth of mature leaves would not lead to dilution.  
210 Ratios of N:CT and N:P were calculated and used as indicators of palatability and  
211 nutritional status, respectively.

212

### 213 Modelling

214

215 Data were analysed separately for each species because we expected responses to be  
216 species-specific (Levick and Rogers 2008). The relationships between browsing  
217 intensity and chemical variables and ratios were explored by testing the fit of linear  
218 ( $y=a+bx$ ), quadratic ( $y=a+bx+cx^2$ ) and bi-quadratic ( $y=a+bx^2+cx^4$ ) models using  
219 TableCurve 2D 5.1 (SYSTAT Software, Inc.) following visual inspections of  
220 scatterplots. Measures of browsing intensity relevant to each species were used  
221 because species were browsed differently (see Results), e.g., the measure of browsing  
222 intensity used in the analysis of *A. grandicornuta* was leaf nibbling because there  
223 were insufficient observations of stem biting to allow the fitting of models. Data were  
224 transformed to  $\log_{10}(y)$ ,  $\log_{10}(x)$ , or  $\log_{10}(x+1)$  when this improved the fit. Only  
225 significant results were considered for presentation. The relationship between

226 elephant impact and chemistry was analysed as a single-factor ANOVA when the  
227 number of trees showing elephant impact permitted such analysis. Trees were  
228 assumed to be replicates within each elephant impact treatment. Therefore, pseudo-  
229 replication constrained the analysis (Underwood 1997). Significance was declared  
230 when  $P < 0.05$ , while possible trends were not ignored when  $0.10 > P > 0.05$ .

231

232

### 233 **Results**

234

235 The type of browsing observed was mostly shoot-biting, except for *A. grandicornuta*,  
236 which was browsed mainly by leaf removal that resulted in almost complete  
237 defoliation below 1.5 m in the most severe cases. Both *C. apiculatum* and *G.*  
238 *flavescens* experienced more browsing by shoot biting than leaf removal, compared to  
239 *A. grandicornuta* (Table 1). *C. apiculatum* and *G. flavescens* were also browsed more  
240 evenly throughout the canopy. *A. grandicornuta* was browsed less by shoot biting  
241 than leaf removal and was mostly browsed below 1.5 m. *D. cinerea* was browsed the  
242 least, of which two-thirds was shoot biting in the upper canopy. While the average  
243 browsing intensity recorded for *A. grandicornuta* was the highest, that of *C.*  
244 *apiculatum* was equivalent to that of *G. flavescens* and 3-fold greater than that of *D.*  
245 *cinerea*. However, maximum browsing intensity was higher for *C. apiculatum* than  
246 either *G. flavescens* or *A. grandicornuta* (Figs 1-3). Browsing impact on *D. cinerea*  
247 never exceeded 10%.

248 *Acacia grandicornuta* – Significant quadratic models were fitted to the  
249 relationships between both [CT] and N:CT in leaves above 1.5 m against the  
250 proportion of productive canopy volume missing below 1.5 m as a result of leaf

251 browsing (Table 2). [CT] was higher at intermediate levels of defoliation compared to  
252 either no defoliation or complete defoliation below 1.5 m, while N:CT was lower at  
253 intermediate levels of defoliation (Fig. 1). A significant bi-quadratic model fitted the  
254 response of [TP] to proportion of productive canopy volume < 1.5 m removed by leaf  
255 browsing (Table 2). [TP] was higher at levels of browsing intensity equivalent to the  
256 removal of 60-80% of foliage below 1.5 m, compared to no defoliation or complete  
257 defoliation below 1.5 m (Fig. 1). [N], [P] and N:P were not significantly related to  
258 browsing intensity ( $P > 0.05$ ). Accumulated elephant impact was not related to  
259 chemical variables ( $P > 0.05$ ).

260 *Combretum apiculatum* – A marginally significant linear model was fitted to  
261 the relationship between [CT] and the total proportion of productive canopy volume  
262 removed by shoot biting (Table 3). [CT] tended to decrease as the total proportion of  
263 productive canopy volume removed by shoot biting increased (Fig. 2). A significant  
264 bi-quadratic model fitted the relationship between [TP] and total proportion of  
265 productive canopy volume removed by shoot biting (Table 3). [TP] was unchanged  
266 when proportion of productive canopy volume removed by shoot biting was 0-20%,  
267 above which it declined to its lowest level when browsing impact was > 50% (Fig. 2).  
268 [N], [P], N:CT and N:P were not significantly related to browsing intensity ( $P > 0.05$ ).  
269 Accumulated elephant impact was not related to chemical variables ( $P > 0.05$ ).

270 *Grewia flavescens* – There were significant linear relationships between both  
271 [P] and [TP] and the total proportion of canopy removed by shoot biting (Fig. 3; Table  
272 4). [P] decreased as browsing intensity increased, but [TP] almost doubled over the  
273 same range of browsing intensity. [N], [CT], N:CT and N:P were not significantly  
274 related to browsing intensity ( $P > 0.05$ ).

275 *Dichrostachys cinerea* – There were no significant relationships between any  
276 of the chemical variables and browsing intensity ( $P > 0.05$ ), probably because of the  
277 very low browsing intensity observed on sampled individuals (Table 1). Shoot biting  
278 was not recorded on half the sampled individuals, while 40% of individuals had <  
279 10% of their canopy volume removed by shoot biting.

280 Notwithstanding the influence of browsing intensity, species varied  
281 substantially in terms of measured chemical variables (Table 5). The species that was  
282 potentially the least palatable was *C. apiculatum*, while *A. grandicornuta* was  
283 potentially the most palatable, in terms of the relative values of [N], [CT] and [TP]. In  
284 contrast, *C. apiculatum* and *A. grandicornuta* were more N-limited than *D. cinerea*  
285 and *G. flavescens* in terms of N:P ratio.

286

287

## 288 **Discussion**

289

290 C-based secondary metabolites and nutrients

291

292 We hypothesised that [CT] and [TP] would decrease, but [N] would increase, in  
293 relation to increasing browsing intensity, leading to woody plants becoming less N-  
294 limited (increased N:P) and hence potentially more palatable (increased N:CT). While  
295 we assumed that the measured chemical traits were primarily responses to mammal  
296 browsing, we also acknowledge their influence on browsing. If innate inter-plant  
297 variation in chemical traits had a strong influence on browsing, this could have biased  
298 our results and influenced our conclusions. However, we assume that browsing effects  
299 are stronger than inter-plant variation. Species-specific responses of [CT], [TP], N:CT

300 and [P] were detected, but [N] and N:P were consistently unvarying. Changes in [P]  
301 were not explicitly included in our hypothesis (P was primarily analysed to calculate  
302 N:P), but a decrease was observed in *G. flavescens*, reasons for which remain unclear.  
303 Our observation that [N] and N:P results did not support our hypothesis suggest that  
304 woody plants in semi-arid savannas, such as the study site, are well adapted to  
305 balancing their N budgets (Ratnam et al. 2008). Alternatively, sampling early in the  
306 wet season may have improved our chances of detecting variations in [N]. The  
307 nutrient dynamics of browsed plants in savannas clearly need to be studied further,  
308 especially in relation to C dynamics. Only the results for [CT] and [TP] in *C.*  
309 *apiculatum* provided some support for our hypothesis. Hence, the main focus of our  
310 discussion is on the contrasting responses of [CT], [TP] and N:CT in *A. grandicornuta*  
311 and [TP] in *G. flavescens*, which failed to support our hypothesis.

312         Various responses to browsing intensity similar to the ones we observed have  
313 been described (Hester et al. 2006), although mechanistic explanations remain  
314 unclear. The hump-shape relationship between secondary metabolites and browsing  
315 intensity in *A. grandicornuta* supports observations elsewhere and can be explained in  
316 terms of C supply (Scogings and Macanda 2005; Kohi et al. 2010). Because most of  
317 the browsing of *A. grandicornuta* was of leaves in the lower canopy (presumably by  
318 impala) we assume that apical dominance was not disrupted (Scogings and Macanda  
319 2005). Therefore, we postulate that C demand did not increase, which allowed CBSM  
320 concentrations to increase because current photosynthate was not allocated to growth  
321 of new shoots. When leaf removal increased further, the number of leaves supplying  
322 C to the pool of C sinks (including the population of current season's shoots, which  
323 we assume did not change) was substantially reduced (Renton et al. 2007; Kohi et al.  
324 2010). Thus, the demand on each leaf for C increased (C limitation), with the result

325 that concentrations of CBSMs decreased such that heavily browsed trees were not  
326 different from lightly browsed trees. It is not clear how species functionally similar to  
327 *A. grandicornuta* respond to increasing intensity of shoot biting throughout the total  
328 canopy. However, severe shoot biting throughout the canopy has been observed to  
329 induce severe C limitation in *Acacia* species (du Toit et al. 1990). In other words,  
330 trees browsed by leaf plucking do not experience severe browsing until browsers are  
331 forced (by food depletion) to switch from leaf plucking to shoot biting. Therefore, we  
332 suggest that potentially palatable, deciduous species with high investment of C in  
333 spines, which are browsed mainly by leaf plucking, are prone to C limitation only  
334 when severe browsing intensity involves substantial shoot biting.

335         Assuming that increasing the intensity of shoot biting reduces apical  
336 dominance and stimulates the growth of new shoots, which increases the demand for  
337 C, we expected to observe a concomitant decrease in concentrations of CBSMs in  
338 leaves (limited supply of C relative to demand) (du Toit et al. 1990; Herms and  
339 Mattson 1992; Skarpe and Hester 2008). The negative relationship between browsing  
340 intensity and both [CT] and [TP] in *C. apiculatum* support observations by Rooke and  
341 Bergström (2007) and corroborate the above hypothesis. In contrast, however, the  
342 increasing [TP] of *G. flavescens* suggests limited demand for C relative to supply,  
343 which supports observations of Bryant et al. (1991) and Palacio et al. (2008). Plants  
344 accumulate C under N limitation (Herms and Mattson 1992). However, *G. flavescens*  
345 plants with elevated [TP] were not obviously N limited because N:P was constant and  
346 within the range indicating optimal nutritional status (Ågren 2008). Alternatively,  
347 plants that are subjected to increasing browsing intensity accumulate C from current  
348 photosynthate or storage (Medhurst et al. 2006; Alcorn et al. 2008; Olesen et al.  
349 2008). The primary C source in *G. flavescens* is not likely storage because the root

350 system is not large; plants are easily uprooted by elephants, revealing shallow roots.  
351 As long as sufficient leaves remain after browsing, photosynthesis contributes more  
352 than stored C to accumulation of C (Medhurst et al. 2006; Olesen et al. 2008).  
353 Compensatory photosynthesis is expected when sink demand for C is increased, e.g.,  
354 when root:shoot ratio is increased and shoot growth is stimulated, but accumulating C  
355 eventually limits photosynthesis (Fernando et al. 2008). Given that photosynthesis  
356 depends on N availability, and our plants were not obviously N stressed, we postulate  
357 that compensatory photosynthesis is more likely than storage to be the primary source  
358 of C in *G. flavescens*, but this remains to be tested. Under the most severe browsing,  
359 compensatory photosynthesis in remaining leaves may not support C accumulation,  
360 leading to reliance on storage (Olesen et al. 2008). Both *C. apiculatum* and *G.*  
361 *flavescens* were browsed at similar intensities by means of shoot biting (presumably  
362 by kudu, giraffe and elephant), but their contrasting responses imply that the effect of  
363 shoot biting (removal of apical buds) is inconsistent among species. Compared to *C.*  
364 *apiculatum*, *G. flavescens* had lower concentrations of CBSMs and higher [N] (Table  
365 5). The contrasting responses of these deciduous, broad-leaved, spineless species  
366 suggest that responses are contingent upon potential palatability.

367

368 Browsing intensity–carbon limitation thresholds

369

370 We outline a conceptual model below to explain diverse species-specific CBSM  
371 responses based on a synthesis of our results and those of related studies in savannas  
372 (Fig. 4). The proposed model builds on the conceptual model previously suggested by  
373 Hester et al (2006). The model is derived from sampling mature leaves for CT or TP  
374 quantification in the middle of the wet season, but serves to illustrate the complexity



375 of browse-browser feedbacks and is an example of the type of functional framework  
376 that can be used for further research. The key concept of the model, however, is that  
377 responses of woody species to browsing may essentially be some form of “hump-  
378 shaped” curve, the parameters of which are determined by factors such as browsing  
379 intensity and resource (water, N) availability in space and time.

380 Our results and those of others suggest that deciduous species with low  
381 allocation of C to CBSMs (e.g., *G. flavescens*) are less prone to C limitation after  
382 browsing than species with high allocation of C to CBSMs (e.g., *C. apiculatum*)  
383 (Bryant et al. 1991). In addition, our observations suggest that deciduous species with  
384 high allocation of C to spines (e.g., *A. grandicornuta*) are less prone to C limitation  
385 after moderately intense browsing than severe browsing. In other words, deciduous  
386 species with high allocation of C to either CBSMs or spines ultimately respond the  
387 same to severe browsing (Fig. 4). Although no evergreen species were included in our  
388 study, they constitute up to 20% of trees in African savannas and are an important  
389 component of browser diets during the dry season (Bergström 1992). It has been  
390 hypothesised that evergreen species have the greatest investment of C in  
391 physical/chemical defence traits (Bryant et al. 1991). Therefore, we hypothesise that  
392 the response of broad-leaf, spiny or spineless, evergreen species in the study area to  
393 increasing intensity of browsing (either leaf plucking switching to shoot biting, or  
394 mainly shoot biting) is C limited. Our conceptual model also predicts that deciduous  
395 species with low investment of C in CBSMs have the strongest capacity to induce  
396 defences under increasing browsing intensity, yet relax defences at very high  
397 browsing intensity because C limitation must eventually take effect.

398 More specifically, the model predicts that potentially palatable species initially  
399 accumulate C through compensatory photosynthesis, but as leaf area declines beyond

400 a threshold of browsing intensity, C becomes limited. In contrast, potentially  
401 unpalatable (N-limited with respect to CBSMs) species do not accumulate C (already  
402 have high investment of C in defences) and experience C limitation at lower  
403 thresholds of browsing intensity. Furthermore, we envisage that responses can be  
404 predicted on the basis of relative allocation of C to total C-based defence traits (e.g.,  
405 spines/thorns, tough/evergreen leaves, phenolic compounds). For example, using leaf  
406 and thorn dry mass fractions of standard-size shoots, and concentrations of total  
407 phenolics and neutral detergent fibre, we estimated that *A. grandicornuta* has less C  
408 allocated to total defence traits compared to *C. apiculatum* at shoot level. The average  
409 fraction of shoot biomass comprising thorns, phenolics and fibre was 26% in *A.*  
410 *grandicornuta*, compared to 34% in *C. apiculatum* (ZSKBP, unpublished data).  
411 However, plants experience substantial temporal variations in resource availability,  
412 which alter the shape of the response (Gayler et al. 2007; Glynn et al. 2007), and  
413 baseline concentrations of CBSMs are low and inducible when resource availability is  
414 high (Bryant et al. 1991; Scogings and Mopipi 2008). Therefore, our model predicts  
415 that the C limitation threshold of browsing intensity in savannas is higher earlier in  
416 the wet season, which is when water and N are most available, than later (Owen-  
417 Smith 2002; Scholes et al. 2003). The predictions outlined above can be readily tested  
418 in multifactorial experiments in which species representing different groups of  
419 functional traits are subjected to at least five levels of each factor (see Scogings and  
420 Mopipi 2008 for further details).

421

422

423 **Conclusions**

424

425 Our study provides a novel demonstration of close links between browsing intensity,  
426 N limitation and C limitation that determine concentrations of CBSMs among woody  
427 plants in African savannas. Both our empirical and predicted responses of CBSMs to  
428 browsing intensity emulate predicted responses of CBSMs to N availability (Herms  
429 and Mattson 1992). Increasing browsing intensity has the same qualitative effect as  
430 decreasing N availability because both factors have similar effects on C source-sink  
431 balances in the plant (either increasing N availability or decreasing browsing intensity  
432 reduces C limitation). The responses to browsing intensity reflect the view that  
433 potentially palatable species are generally more likely to show initial induction of  
434 defence traits at low to moderate browsing intensities, depending on resource  
435 availability. Therefore, the browsing intensity at which C limitation takes effect  
436 depends on (i) the amount of total C invested in all C-based (physical + chemical)  
437 defence traits, and (ii) N availability. Predictions have been derived about interactions  
438 between the effects of browsing intensity and N availability on the potential  
439 nutritional value of forage for browsing mammals, but they remain to be tested. This  
440 is important to do because, although resource availability is known to be highly  
441 variable across all spatial/temporal scales in African savannas, understanding the  
442 influence of such variation on browse-browser interactions has been neglected  
443 (Levick and Rogers 2008).

444

445

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455

456

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617

618

619 **Figure legends**

620

621 **Fig. 1** Condensed tannin (CT), nitrogen:condensed tannin ratio (N:CT) and total  
622 polyphenol (TP) concentrations in mature leaves above 1.5 m on *A. grandicornuta*  
623 taller than 2 m at Nkuhlu, 28-30 January 2008, in relation to browsing intensity (%)  
624 expressed as the proportion of productive canopy volume missing below 1.5 m due to  
625 leaf removal. Maximum browsing impact in this situation represents almost complete  
626 defoliation below 1.5 m. Significant quadratic models ( $y=a+bx+cx^2$ ) were fitted for  
627 responses of both  $\log_{10}$  (CT) ( $r^2 = 0.24$ ;  $F_{2,32} = 5.05$ ;  $P = 0.012$ ) and N:CT ( $r^2 = 0.24$ ;  
628  $F_{2,27} = 4.34$ ;  $P = 0.023$ ). A significant bi-quadratic model ( $y=a+bx^2+cx^4$ ) was fitted  
629 for the response of  $\log_{10}$  (TP) ( $r^2 = 0.25$ ;  $F_{2,32} = 5.24$ ;  $P = 0.011$ ). Model parameters  
630 are given in Table 2. Note log scales

631

632 **Fig. 2** Condensed tannin (CT) and total polyphenol (TP) concentrations in mature  
633 leaves above 1.5 m on *C. apiculatum* taller than 2 m at Nkuhlu, 28-30 January 2008,  
634 in relation to browsing intensity (%) expressed as the proportion of productive canopy  
635 volume removed by shoot biting. A marginally significant linear model ( $y=a+bx$ ) was  
636 fitted for the response of  $\log_{10}$  (CT) ( $r^2 = 0.11$ ;  $F_{1,32} = 3.80$ ;  $P = 0.060$ ) and a  
637 significant bi-quadratic model ( $y=a+bx^2+cx^4$ ) was fitted to the response of  $\log_{10}$  (TP)  
638 ( $r^2 = 0.26$ ;  $F_{2,29} = 5.15$ ;  $P = 0.012$ ). Model parameters are given in Table 3. Note log  
639 scales

640

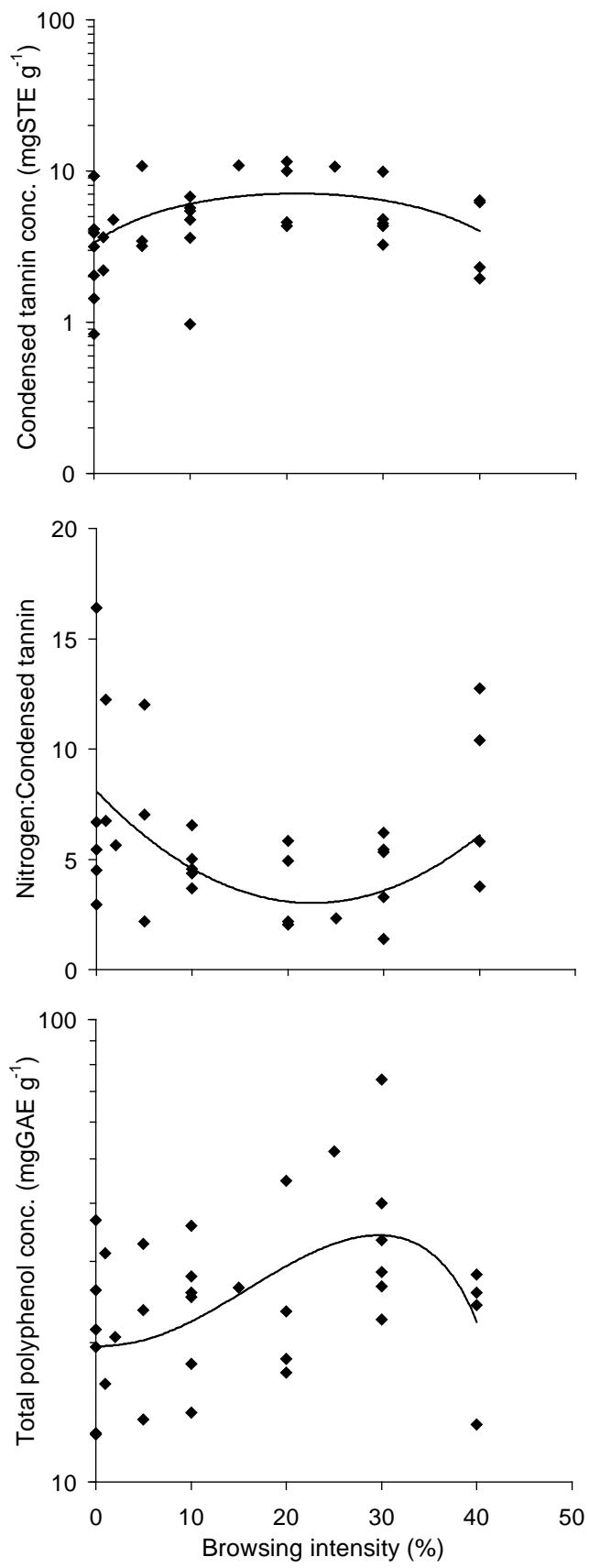
641 **Fig. 3** Phosphorus (P) and total polyphenol (TP) concentrations in mature leaves  
642 above 1.0 m on *G. flavescens* taller than 1.5 m at Nkuhlu, 28-30 January 2008, in  
643 relation to browsing intensity (%) expressed as the proportion of productive canopy

644 volume removed by shoot biting. Significant linear models ( $y=a+bx$ ) were fitted for  
645  $\log_{10}$  (P) ( $r^2 = 0.47$ ;  $F_{1,23} = 20.17$ ;  $P < 0.001$ ) and  $\log_{10}$  (TP) ( $r^2 = 0.36$ ;  $F_{1,22} = 12.56$ ;  
646  $P = 0.002$ ). Model parameters are given in Table 4. Note log scales

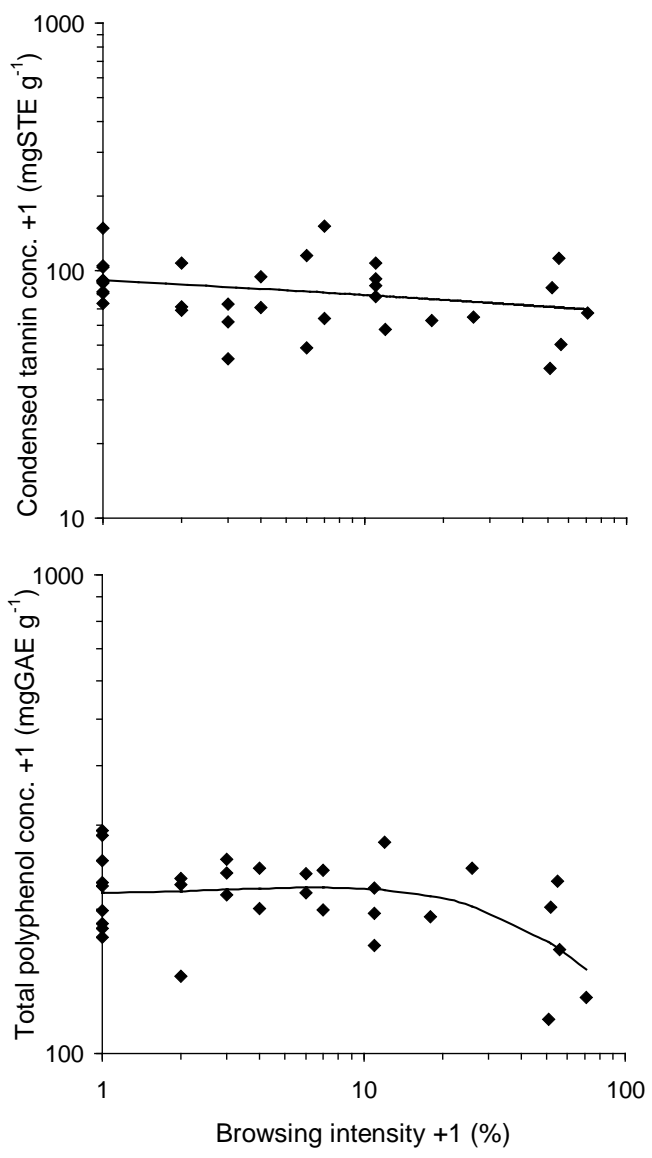
647

648 **Fig. 4** Hypothesised responses of four broad functional groups of woody species to  
649 browsing in African savannas. All species eventually become C limited. Increasing N  
650 availability is thought to induce an upwards (rightwards) shift in the browsing  
651 intensity threshold at which CBSMs start to decrease (Gayler et al. 2007). Species in  
652 group (i) are assumed to have the lowest relative allocation of C to putative defence  
653 traits and respond to increasing browsing intensity by increasing CBSM  
654 concentrations, but ultimately become C-limited and reduce CBSM concentrations.  
655 Species in group (ii) are assumed to have intermediate relative investment of C in  
656 putative defence traits and respond by increasing CBSM concentrations, but relax  
657 them at high browsing intensity because of C limitation. Species in group (iii) are  
658 assumed to have high relative investment of C in putative defence traits and respond  
659 by decreasing CBSM concentrations. Species in group (iv) are assumed to have the  
660 highest relative allocation of C to putative defence traits and also respond by  
661 decreasing CBSM concentrations, but the range of values is high. It is feasible that  
662 spines follow the same pattern if severe browsing leads to C-starvation. Responses of  
663 spines have been mainly studied in *Acacia* species, showing increased spinescence  
664 (e.g., Fornara and du Toit 2007; Goheen et al. 2007; Zinn et al. 2007), but thorns of  
665 *Balanites glabra* are green, modified shoots, which became shorter under severe  
666 browsing because browsing induces early maturation (Milewski and Madden 2006).  
667 Spinescence has not been studied in relation to browsing intensity

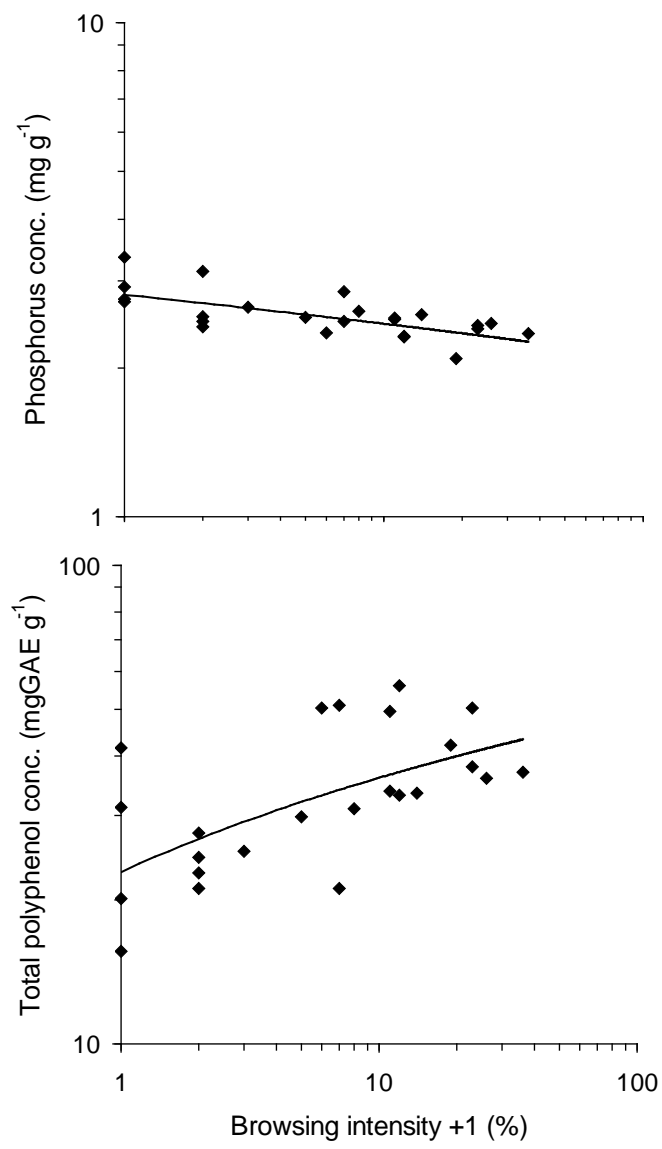
## Figures



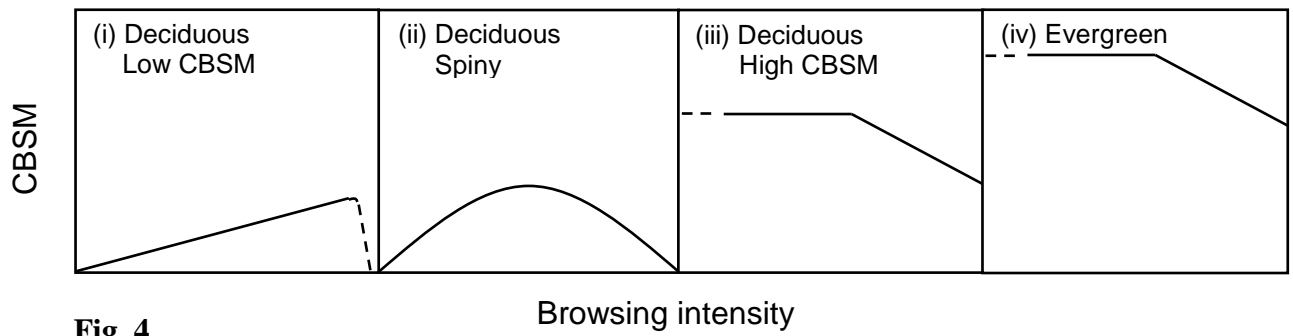
**Fig. 1**



**Fig. 2**



**Fig. 3**



**Fig. 4**



## Tables

**Table 1** Average proportion (%) of productive canopy volume estimated to be missing due to leaf removal below 1.5 m and above 1.5 m, and accumulated shoot biting below 1.5 m and above 1.5 m, recorded for individuals of the study species sampled at 36 sites per species at Nkuhlu, 28-30 January 2008

Species	Leaf removal			Shoot biting		
	<1.5 m	>1.5 m	Sum	<1.5 m	>1.5 m	Sum
<i>A. grandicornuta</i>	15.4	0.6	16.0	6.1	1.8	7.9
<i>C. apiculatum</i>	1.9	0.2	2.1	9.1	2.3	11.4
<i>G. flavescens</i> *	2.6	3.0	5.6	3.9	4.6	8.5
<i>D. cinerea</i>	0.0	0.1	0.1	1.3	2.8	4.1

\* Only 24 individuals were sampled because plants fitting the selection criteria could not be found at 12 sites

**Table 2** Parameters of the quadratic models ( $y=a+bx+cx^2$ ) fitted to the responses of  $\log_{10}$ (condensed tannin concentration) ( $\log_{10}$ [CT]) and N:CT ratio, and the bi-quadratic model ( $y=a+bx^2+cx^4$ ) fitted to the response of  $\log_{10}$ (total polyphenol concentration) ( $\log_{10}$ [TP]), in mature leaves above 1.5 m to the proportion (%) of productive canopy volume missing below 1.5 m as a result of leaf browsing on *A. grandicornuta* taller than 2 m at Nkuhlu, 28-30 January 2008

Response	a	b	c	SE	t	P	n*
$\log_{10}$ [CT]	0.43986			0.082311	5.34	<0.001	34
		0.03606		0.011899	3.03	0.005	34
			-0.00081	0.000308	-2.64	0.012	34
N:CT	8.08232			1.071131	7.54	<0.001	29
		-0.44793		0.152123	-2.94	0.007	29
			0.01108	0.003870	2.86	0.008	29
$\log_{10}$ [TP]	1.293318			0.040426	31.91	<0.001	34
		0.000567		0.000178	3.18	0.003	34
			$-3.3 \times 10^{-7}$	$-1.17 \times 10^{-7}$	2.85	0.008	34

\* n varies because of missing values in the data set

**Table 3** Parameters of the linear model ( $y=a+bx$ ) fitted to the response of  $\log_{10}$ (condensed tannin concentration) ( $\log_{10}$ [CT]) and the bi-quadratic model ( $y=a+bx^2+cx^4$ ) fitted to the response of  $\log_{10}$ (total polyphenol concentration) ( $\log_{10}$ [TP]) in mature leaves above 1.5 m to  $\log_{10}$ (proportion of productive canopy volume missing as a result of shoot browsing +1) for *C. apiculatum* taller than 2 m at Nkuhlu, 28-30 January 2008

Response	a	b	c	SE	t	P	n*
$\log_{10}$ [CT]	1.94987			0.033446	58.30	<0.001	33
		-0.07088		0.036357	-1.95	0.060	33
$\log_{10}$ [TP]	2.33617			0.021736	107.47	<0.001	31
		0.03171		0.050038	0.63	0.531	31
			-0.02297	0.015843	-1.45	0.158	31

\* n varies because of missing values in the data set

**Table 4** Parameters of linear models ( $y=a+bx$ ) fitted to (a) the response of  $\log_{10}$ (phosphorus concentration) to  $\log_{10}$ (total proportion of productive canopy volume removed by shoot browsing +1), and (b) the response of  $\log_{10}$ (total polyphenol concentration) to  $\log_{10}$ (total proportion of productive canopy volume removed by shoot browsing +1) for *G. flavescens* at Nkuhlu, 28-30 January 2008. All chemical values are for mature leaves above 1.0 m on *G. flavescens* taller than 1.5 m

Model	a	b	SE	<i>t</i>	<i>P</i>	<i>n</i>
(a)	0.45		0.012	39.09	<0.001	25
		-0.06	0.013	-4.49	<0.001	25
(b)	1.38		0.045	30.49	<0.001	24
		0.18	0.050	3.54	0.002	24

**Table 5** Mean concentrations (SEM and sample size in parentheses) of total polyphenols (TP), condensed tannins (CT) and nutrients (mg g<sup>-1</sup>) of trees sampled at Nkuhlu, 28-30 January 2008

Species	TP <sup>#</sup>	CT <sup>##</sup>	N	P	N:CT	N:P
<i>A. grandicornuta</i>	26.3 <sup>†</sup> (2.12; 35)	5.5 <sup>†</sup> (0.63; 35)	25.7 (0.79; 32)	2.5 (0.05; 32)	7.7 <sup>†</sup> (1.42; 32)	10.1 (0.29; 32)
<i>C. apiculatum</i>	213.1 <sup>†</sup> (7.33; 32)	83.3 <sup>†</sup> (4.43; 34)	22.4 (0.59; 34)	2.3 (0.05; 34)	0.3 (0.02; 34)	9.8 (0.29; 34)
<i>D. cinerea</i>	68.8 (3.85; 35)	38.1 (2.31; 36)	30.7 (0.76; 36)	2.4 (0.06; 36)	0.9 (0.06; 36)	13.2 (0.41; 36)
<i>G. flavescens</i>	34.3 <sup>†</sup> (2.31; 24)	35.4 (1.88; 25)	34.1 (1.14; 25)	2.6 <sup>†</sup> (0.05; 25)	1.1 (0.08; 25)	13.4 (0.55; 25)

† Browsing intensity effect was significant ( $P < 0.05$ ); see Figures 1-3 and Tables 2-4

# Gallic acid equivalents

## Sorghum tannin equivalents