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1 **Secondary metabolites and nutrients of woody plants in relation to**

2 **browsing intensity in African savannas**

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

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

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Introduction

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

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

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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

4

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.

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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^{-2}, 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 detectible 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^{-1} 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

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

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

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

Conclusions

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

457   **References**

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617

618

Figure legends

Fig. 1 Condensed tannin (CT), nitrogen:condensed tannin ratio (N:CT) and total

polyphenol (TP) concentrations in mature leaves above 1.5 m on *A. grandicornuta*

taller than 2 m at Nkuhlu, 28-30 January 2008, in relation to browsing intensity (%)

expressed as the proportion of productive canopy volume missing below 1.5 m due to

leaf removal. Maximum browsing impact in this situation represents almost complete

defoliation below 1.5 m. Significant quadratic models ($y=a+bx+cx^2$) were fitted for

responses of both $\log_{10}$ (CT) ($r^2 = 0.24$; $F_{2,32} = 5.05$; $P = 0.012$) and N:CT ($r^2 = 0.24$;

$F_{2,27} = 4.34$; $P = 0.023$). A significant bi-quadratic model ($y=a+bx^2+cx^4$) was fitted

for the response of $\log_{10}$ (TP) ($r^2 = 0.25$; $F_{2,32} = 5.24$; $P = 0.011$). Model parameters

are given in Table 2. Note log scales

Fig. 2 Condensed tannin (CT) and total polyphenol (TP) concentrations in mature

leaves above 1.5 m on *C. apiculatum* taller than 2 m at Nkuhlu, 28-30 January 2008,

in relation to browsing intensity (%) expressed as the proportion of productive canopy

volume removed by shoot biting. A marginally significant linear model ($y=a+bx$) was

fitted for the response of $\log_{10}$ (CT) ($r^2 = 0.11$; $F_{1,32} = 3.80$; $P = 0.060$) and a

significant bi-quadratic model ($y=a+bx^2+cx^4$) was fitted to the response of $\log_{10}$ (TP)

($r^2 = 0.26$; $F_{2,29} = 5.15$; $P = 0.012$). Model parameters are given in Table 3. Note log

scales

Fig. 3 Phosphorus (P) and total polyphenol (TP) concentrations in mature leaves

above 1.0 m on *G. flavescens* taller than 1.5 m at Nkuhlu, 28-30 January 2008, in

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).

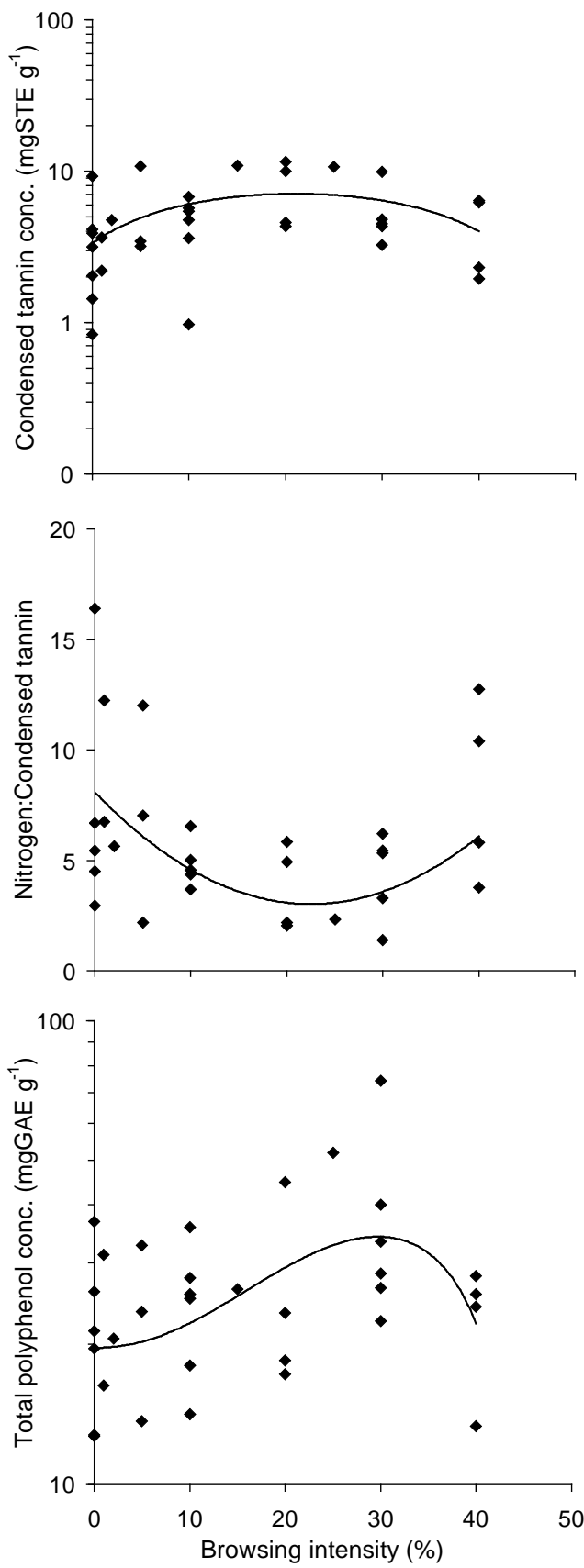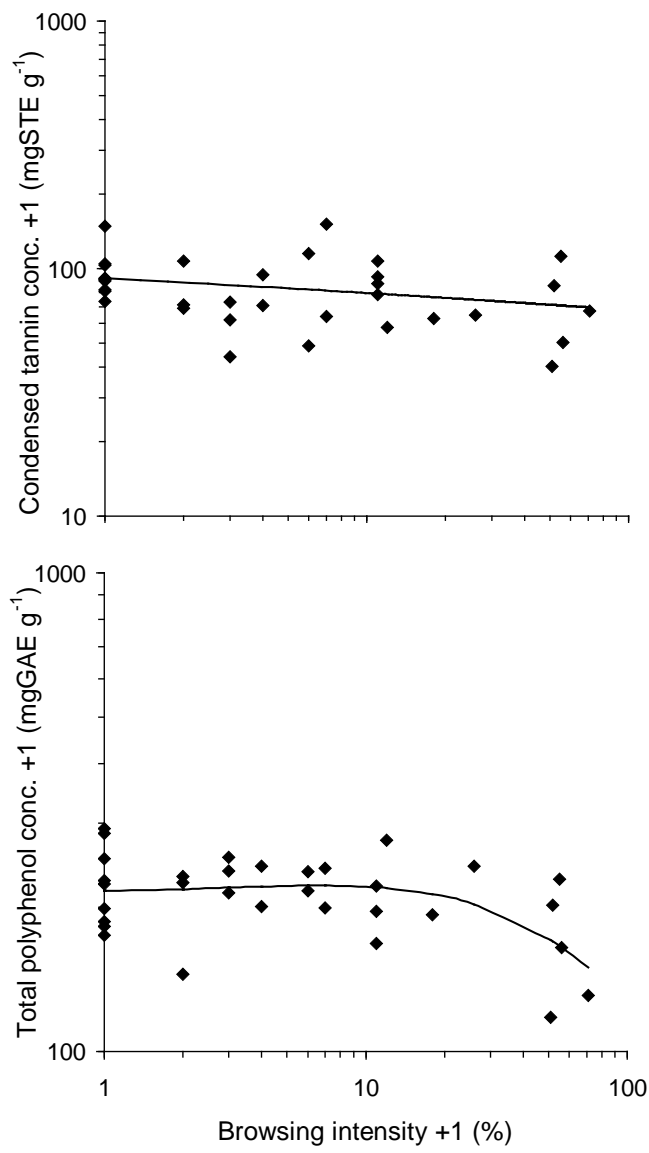667   Spinescence has not been studied in relation to browsing intensity
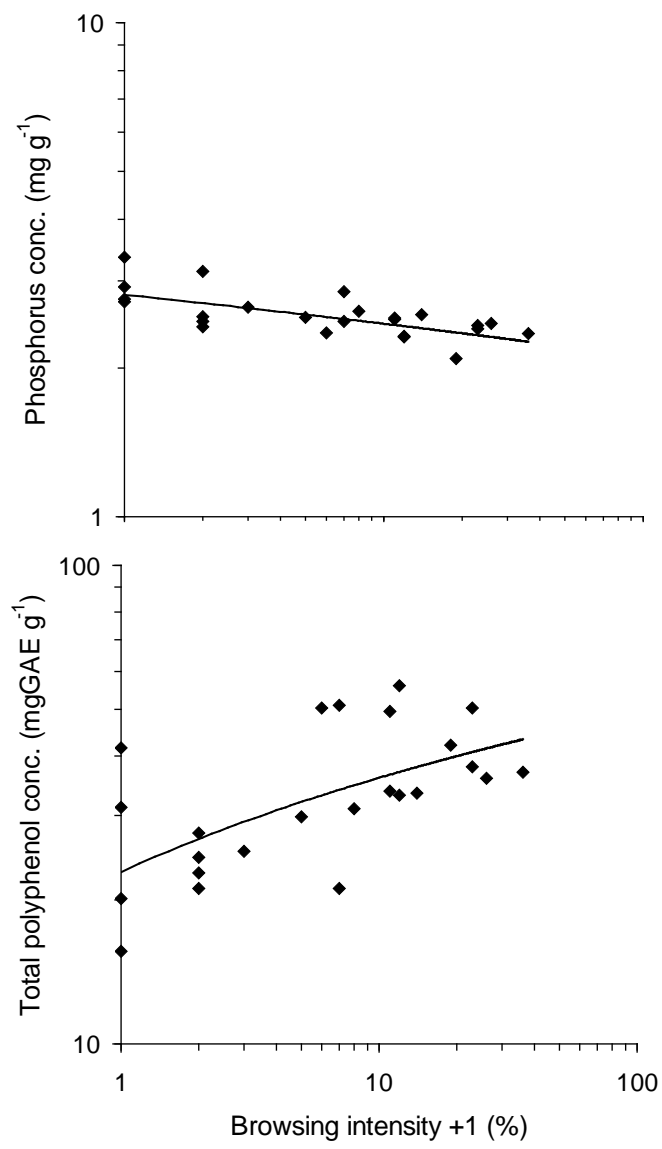
Figures

Fig. 1

Fig. 2

Fig. 3

Fig. 4

(i) Deciduous Low CBSM (ii) Deciduous Spiny (iii) Deciduous High CBSM (iv) Evergreen
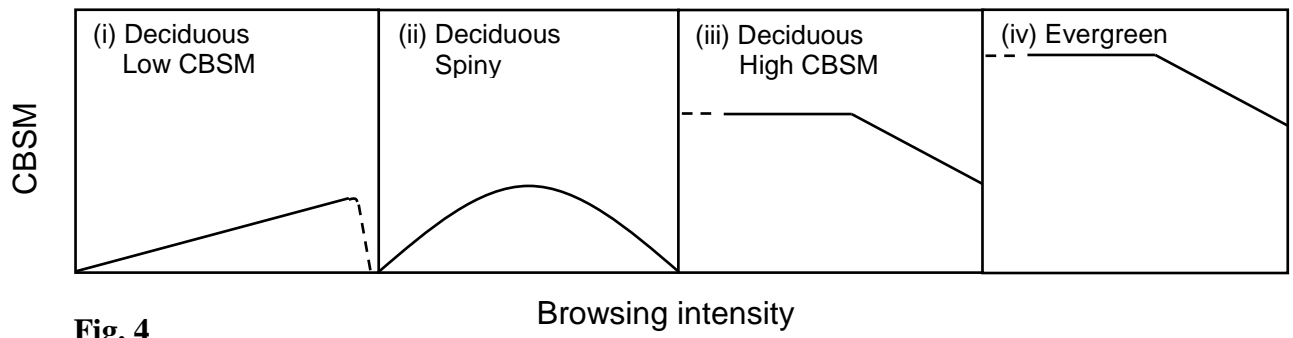
CBSM

Browsing intensity

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
A. grandicornuta	15.4	0.6	16.0	6.1	1.8	7.9
C. apiculatum	1.9	0.2	2.1	9.1	2.3	11.4
*G. flavescens**	2.6	3.0	5.6	3.9	4.6	8.5
D. cinerea	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
			-3.3×10^{-7}	-1.17×10^{-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	*t*	*P*	*n*
(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^{-1}) of trees sampled at Nkuhlu, 28-30 January 2008

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