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1 **Does large herbivore removal affect secondary metabolites, nutrients**

2 **and shoot length in woody species in semi-arid savannas?**

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Abstract

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27 We hypothesised that exclusion of long-term browsing leads to decreased nutrient

28 concentrations, increased carbon-based secondary metabolites (CBSMs) and

29 decreased shoot length in woody plants in semi-arid savannas. To test this, we

30 sampled four deciduous woody species in a large-scale, long-term exclusion

31 experiment. We found a tendency for large herbivore exclusion to either decrease

32 nitrogen or increase tannin in two tree species. Phosphorus and total polyphenol

33 responses indicated complex interactions with herbivore assemblage. Shoot length

34 decreased under exclusion in two species, while a similar tendency existed in the

35 remaining species. Therefore, we found limited support for our predictions that

36 exclusion of browsing results in reduced nitrogen or increased CBSMs, but moderate

37 support for decreased shoot length in semi-arid savannas. *Dichrostachys cinerea*, a

38 fast-growing, aggressive invader in savannas, displayed C-limitation with removal of

39 large herbivores because both shoot length and CBSMs decreased. In conclusion,

40 effects of long-term browsing on deciduous trees in semi-arid savannas depend on the

41 plant species, specific nutrients or CBSMs measured and the composition of the

42 herbivore assemblages. Because elephant densities in the study area were high and

43 most responses were associated with their exclusion, we conclude that elephants are

44 important drivers of browse quality in the study area.

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46 *Keywords:* Elephant, Exclusion experiment, Nitrogen, Phenol, Plant defence, Tannin

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1. Introduction

Plant species display various combinations of physical and chemical traits that have evolved in response to selection by environmental conditions. Some of these traits enhance the fitness of plants in response to herbivores because the traits either reduce the rate of consumption, or increase the rate of regrowth (Briske, 1996). These traits are regarded as constituting broad strategies of avoidance and tolerance, which are not mutually exclusive and are collectively known as herbivore resistance (Herms and Mattson, 1992; Stevens et al. 2007; Skarpe and Hester, 2008). Plant communities comprise mixtures of species, each displaying a range of strategies contingent on fluctuations in herbivore impacts and environmental factors (Hjältén et al., 1996; Hester et al., 2006). Understanding how individual plant species respond to herbivores in semi-arid savannas is critical for understanding how plant assemblages respond to changing environments (Hester et al., 2006).

Carbon-based secondary metabolites (CBSMs), such as tannins, are assumed to function as chemical defences that contribute to herbivore-avoidance strategies (Bryant et al., 1985; Skarpe and Hester, 2008). The concentration of CBSMs in individual plants depends on resource availability in the environment (Koricheva et al., 1998; Stevens et al., 2007) and the effect that herbivores have on resource allocation and availability in plants (Nykanen and Koricheva, 2004; Ballare, 2011; Orians et al., 2011). Plant responses to herbivores may also depend on the severity of damage (Hjältén et al., 1993, 1994; Nykanen and Koricheva, 2004).

A major component of research in semi-arid savannas concerns the effects of large herbivores (especially elephants) on woody vegetation, with the ultimate objective being the development of improved management policies (O'Keefe and Alard, 2002).

3

76   While defoliation may induce defences in woody plants in semi-arid savannas (Ward

77   and Young, 2002), severe browsing by large herbivores in savannas has been reported

78   to maintain elevated shoot growth associated with increased N concentrations or

79   reduced tannin concentrations in individual plants (du Toit et al., 1990). Heavily

80   browsed plants that have switched to a vegetative state characterised by N-rich/C-poor

81   tissues are in positive feedback loops because the switch increases the probability of

82   browsing (Fornara and du Toit, 2007; Skarpe and Hester, 2008). One possible

83   explanation for reduced CBSMs in browsed plants is a relative increase in allocation

84   of C to growth of new shoots rather than CBSMs (Fornara and du Toit, 2007; Hrabar

85   et al., 2009), which can occur if the root:shoot ratio is altered such that shoot growth

86   increases (Herms and Mattson, 1992; Renton et al., 2007). Evidence for the responses

87   of nutrients and CBSMs to long-term browsing in semi-arid savannas is inconsistent,

88   but shoot growth rates consistently increase (Ward and Young, 2002; Fornara and du

89   Toit, 2007; Hrabar et al., 2009).

90   Our objective was to study the effects of large herbivore exclusion on woody

91   species in terms of (i) condensed tannin (CT), total polyphenol (TP), N and P

92   concentrations in mature leaves and (ii) shoot length. The premise of this approach is

93   that exclusion of herbivores allows their effects to be determined (O'Keefe and Alard,

94   2002). Mature leaves comprise the main component of foliage in all browsers' diets

95   for most of the growing season. Therefore, browsers would potentially be affected by

96   changes in mature leaves rather than young leaves that are only briefly available early

97   in the wet season. Although the response of shoot length to browsing is unlikely to be

98   directly related to total shoot biomass because the number of shoots is often reduced

99   by browsing (Bergström et al., 2000), the response of shoot length in *Acacia* trees has

100   been found to be comparable to that of total shoot productivity (Milton, 1988;

4

101 Dangerfield and Modukanele, 1996; Fornara and du Toit, 2007). In addition, neither

102 shoot length nor total shoot growth necessarily reflect total plant growth because they

103 are the result of resources being allocated to adjust the root:shoot ratio (Teague, 1985;

104 Teague & Walker, 1988). Consistent with responses commonly reported in the

105 literature (e.g., du Toit et al., 1990, Ward & Young, 2002; Fornara & du Toit, 2007)

106 we postulated that concentrations of CBSMs are increased, but nutrient concentrations

107 decreased, in plants under herbivore exclusion compared to plants under long-term

108 browsing. We also expected shoot length to be shorter in plants under herbivore

109 exclusion compared to browsed plants (Hrabar et al., 2009). We tested the above

110 hypotheses by sampling four woody species within a large-scale, long-term exclusion

111 experiment established in 2002 in a semi-arid savanna in Kruger National Park, South

112 Africa.

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115 **2. Material and methods**

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117 2.1. Study area

118

119   The Nkuhlu Large-scale Long-term Exclusion Experiment (24° 58′ S, 31° 46′ E) is

120 adjacent to the Sabie River, Kruger National Park, South Africa (O'Keefe and Alard,

121 2002). The climate is semi-arid subtropical with two broadly distinct seasons: a hot,

122 occasionally wet, growth season (October-April) and a warm, dry, non-growing

123 season (Williams et al., 2009). Mean annual rainfall at Skukuza, 30 km west of

124 Nkuhlu, is ~550 mm. Average daily temperatures at Skukuza are 15.7 °C in June and

125 26.6 °C in January. Average minimum temperature in June is 5.7 °C and average

126   maximum temperature in January is 32.6 °C. Altitude is 200-230 m above mean sea

127   level. Topography comprises undulating landscape derived from granite. Crests and

128   middle slopes are characterized by shallow, sandy, coarse soil, while footslopes are

129   characterized by deep, sodic, duplex soil (Khomo and Rogers, 2005; Grant and

130   Scholes, 2006). Sodic soils are regarded as stressful environments for vegetation,

131   which is sparse, but regarded as more nutritious than crest vegetation to large

132   herbivores (Tarasoff et al., 2007; Levick and Rogers, 2008).

133   Abundant woody species (Schmidt et al., 2007) include *Acacia grandicornuta* and

134   *Euclea divinorum* on the footslopes, and *Dichrostachys cinerea*, *Acacia exuvialis*,

135   *Combretum apiculatum* and *Grewia flavescens* on the middle slopes and crests

136   (Siebert and Eckhardt, 2008). Most of the woody species are deciduous and shorter

137   than 10 m. Common mammal herbivores (Skinner and Chimimba, 2005) include

138   impala (*Aepyceros melampus*), African elephant (*Loxodonta africana*), hippo

139   (*Hippopotamus amphibius*), black rhino (*Diceros bicornis*), white rhino

140   (*Ceratotherium simum*), greater kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa

141   camelopardalis*), steenbok (*Raphicerus campestris*), scrub hare (*Lepus saxatilis*), blue

142   wildebeest (*Connochaetes taurinus*), Cape buffalo (*Syncerus caffer*) and plains zebra

143   (*Equus quagga*). Elephant, impala, black rhino, kudu, giraffe and steenbok are the

144   main consumers of woody vegetation in the study area. Elephant density fluctuates

145   around 0.5-2.0 individuals/km^2 (Grant et al., 2008). A breeding herd of 30-40 impala,

146   several impala bachelors, two black rhino and an unknown number of steenbok are

147   resident in the study area, while low numbers of giraffe and kudu are occasionally

148   present.

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150   2.2. Sampling

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152   The Nkuhlu Large-scale Long-term Exclusion Experiment comprises one

153   exclusion plot (70 ha) that excludes all herbivores the size of hares and larger (total

154   exclusion) and one exclusion plot (44 ha) that excludes elephants, but not other

155   herbivores (partial exclusion). The two exclusion plots, established in 2002, are

156   separated by a control area (25 ha) open to all large herbivores (no exclusion).

157   Treatments could not be replicated because of the large scale of the experimental plots

158   (Levick and Rogers, 2008; Jonsson et al., 2010). If excluding either elephants or all

159   large herbivores shows similar responses then it can be inferred that the main source

160   of the effect is elephants (Jonsson et al., 2010). If excluding elephants shows a

161   different response to excluding all large herbivores then it can be inferred that the

162   main source of the effect is not elephants.

163   The plant species selected were among the most abundant and evenly distributed

164   in the study area, allowing for the desired sampling strategy to be implemented. The

165   species were *Acacia grandicornuta* Gerstner, *Dichrostachys cinerea* (L.) Wright and

166   Arn. subsp. *africana* Brennan and Brummitt (hereafter simply *D. cinerea*),

167   *Combretum apiculatum* Sond. and *Grewia flavescens* Juss. *Acacia grandicornuta* is a

168   deciduous legume with fine, bi-compound leaves and long straight spines in pairs at

169   the nodes. *Dichrostachys cinerea* is a multi-stemmed, deciduous legume with fine, bi-

170   compound leaves and stem-spines (short shoots that have sharp tips). Both *C.*

171   *apiculatum* and *G. flavescens* are deciduous and broad-leaved, but *C. apiculatum* is a

172   tree, while *G. flavescens* is a many-stemmed large shrub. Sampling was scheduled

173   according to preliminary observations in two previous years at the site, which

174   indicated that effects of browsing on CTs and TPs of mature leaves were most readily

175   detected in the middle of the wet season (Zululand/Sweden Kruger Browse Project -

176   ZSKBP, unpublished data). Sampling leaves for chemical analysis in January was

177   appropriate because CTs and TPs are thought to accumulate as the season progresses

178   (Barton and Koricheva, 2010). Our preliminary data also indicated that sampling in

179   the middle of the wet season was suitable for detecting effects of browsing on

180   nutrients. Sampling only mature leaves at one time ensured that leaf phenology would

181   not confound our results. A 30 x 30 m grid was used to randomly locate 18 sites on

182   the crest and 18 on the footslope in each plot (54 sites altogether per catena position).

183   One tree of each study species was sampled in each grid cell on condition that it was

184   (i) closest to the grid-cell centre, (ii) taller than 2 m, and (iii) neither obviously

185   stressed by disease, disturbance or neighbours nor obviously growing in a nutrient

186   enriched patch. The minimum height of selected *G. flavescens* plants was 1.5 m

187   because it seldom grew taller than 2 m. If any condition was not met for the closest

188   tree, then the next closest tree meeting the conditions was sampled. No tree was

189   sampled if the closest suitable tree was > 15 m from the grid-cell centre. The total

190   number of sampled trees was 196, comprising 53 *A. grandicornuta*, 49 *C. apiculatum*,

191   53 *D. cinerea* and 41 *G. flavescens*.

192   Samples were collected on 28-30 January 2008 by clipping branches 3-8 mm in

193   diameter from the northern, sunlit half of the canopy 1.5-2.2 m above ground, which

194   was within reach of most browsers in the study area. For *G. flavescens*, the lowest

195   permissible height for collection was 1.0 m because of its low stature. Branches were

196   collected 1-4 hours after sunrise (05:25). Mature leaves that did not show signs of

197   severe insect herbivory were removed for drying at 60 °C for 24 hours. Each dried

198   sample of leaves was milled (1.0 mm) and then analysed for concentrations of

199   condensed tannins ([CT]) (Porter et al., 1986), total polyphenols ([TP]) (Price and

200   Butler, 1977), Kjeldahl-N ([N]) (AOAC, 1990) and phosphorus ([P]) (Murphy and

201 Riley, 1962). All concentrations were expressed in mg/g dry mass. [CT] and [TP]

202 were expressed as sorghum tannin equivalents (STE) and gallic acid equivalents

203 (GAE), respectively. Differences in concentrations were assumed to reflect

204 differences in absolute amounts because the limited growth of mature leaves would

205 not lead to dilution.

206   Preliminary observations in the study area in previous years indicated that effects

207 of browsing on current season shoot growth were most readily detected early in the

208 wet season (ZSKBP, unpublished data). The shoots on all the species started growing

209 a week after the first rainfall and continued for up to 6 weeks, so measuring shoot

210 length at one time early in the season reflected maximum growth rate. Shoot growth

211 could not be measured later in the wet season because most current season shoots

212 were no longer intact. Therefore, the lengths of 10 randomly selected current season

213 shoots were measured on each of five randomly selected trees per species on 5-6

214 November 2007. The length of each new shoot was measured from its base to the base

215 of the apical bud.

216

217 2.3. Statistical analyses

218

219   Data were analysed separately for each species. To fulfil the requirement of

220 normality and equal variances, all chemical data were $\log_{10}$ transformed, while

221 average shoot length per tree was square-root transformed for *A. grandicornuta* and

222 $\log_{10}$ transformed for *C. apiculatum*, *G. flavescens* and *D. cinerea*. The effect of

223 treatment on each chemical and growth variable was analysed as a single-factor

224 ANOVA, assuming trees were replicates within each treatment. Therefore, pseudo-

225 replication constrained the analysis and the estimates of model parameters should be

9

226   viewed with caution (Underwood, 1997). During the analysis of *G. flavescens*, it

227   appeared that there were two populations that differed in [CT], such that one

228   population had higher [CT] than the other. The two populations were subsequently

229   assumed to represent two varieties, namely var. *flavescens* and var. *olukondae*

230   (Schinz.), of which the latter was not expected in the study area (Schmidt et al., 2007).

231   Close examination of sampled plants in the field with the benefit of hindsight

232   indicated that the more abundant, low-CT (< 37 mg/g) plants had smoother, softer

233   leaves characteristic of var. *olukondae*, while the less abundant, high-CT (> 42 mg/g)

234   plants had rougher, harder leaves characteristic of var. *flavescens*. Effects of exclusion

235   on [CT] were therefore analysed for the two varieties separately. Significance was

236   declared when $P < 0.05$, while possible trends were not ignored when $0.10 > P > 0.05$.

237   From an environmental management perspective, it is better to relax P and make a

238   Type I error when the statistical power of the experiment is not strong, than to make a

239   Type II error in accepting the null hypothesis when it is false (Underhill, 1997).

240

241

242   **3. Results**

243

244   Each species that we studied expressed at least one chemical response to exclusion

245   of large herbivores. For *A. grandicornuta*, exclusion treatments negatively affected

246   [N] ($F_{2,47} = 3.89$; $P = 0.027$), but had no effect on other chemical variables ($P > 0.05$)

247   (Fig. 1). For *C. apiculatum*, exclusion increased [CT] ($F_{2,46} = 8.76$; $P = 0.001$), but did

248   not significantly affect other chemical variables ($P > 0.05$) (Fig. 1). In *D. cinerea*,

249   [TP] tended to be lowest in the partial exclusion plot and highest in the control plot

250   ($F_{2,49} = 3.10$; $P = 0.054$), while there were no significant effects on the other chemical

251   variables ($P > 0.05$) (Fig 1).

252   In *G. flavescens*, partial exclusion of large herbivores increased [P] ($F_{2,38} = 4.57$; P

253    $= 0.017$), but did not affect other chemical variables ($P > 0.05$), except that a

254   marginally significant negative effect was noted for [TP] ($F_{2,37} = 2.67$; $P = 0.083$)

255   (Fig. 1). Analysis of var. *olukondae* produced a significant positive effect of exclusion

256   ($F_{2,26} = 3.32$; $P = 0.052$), where mean [CT] was 31.5 mg/g (SEM: 1.79) in the partial

257   exclusion plot, 32.0 mg/g (SEM: 1.13) in the total exclusion plot and 27.4 mg/g

258   (SEM: 1.34) in the control plot.

259   Notwithstanding the effects of large herbivores, tree species varied substantially in

260   terms of measured chemical variables (Fig. 1) as well as in shoot length. *Acacia*

261   *grandicornuta* had 4-8 times longer shoots than other species. Shoot length of *D.*

262   *cinerea* ($F_{2,11} = 12.23$; $P = 0.002$) and *A. grandicornuta* ($F_{2,11} = 6.60$; $P = 0.013$) were

263   shorter under total exclusion, but *C. apiculatum* ($F_{2,12} = 2.02$; $P = 0.175$) and *G.*

264   *flavescens* ($F_{2,12} = 1.68$; $P = 0.235$) were not affected (Fig. 2). Total exclusion reduced

265   shoot length by 50% and 46% for *D. cinerea* and *A. grandicornuta* respectively.

266

267

268   **4. Discussion**

269

270   The hypothesis that concentrations of CBSMs increase, but nutrient concentrations

271   decrease, in plants after removal of large herbivores in semi-arid savannas received

272   limited support. In no species did concentrations of both CBSMs and nutrients change

273   together. Either one CBSM increased or one nutrient decreased in two of the four

274   study species when herbivores were excluded, suggesting the presence of positive

275 feedback loops between large herbivores and trees of some species. While responses

276 of [N] and [CT] suggested elephant browsing has the potential to initiate positive

277 feedback in semi-arid savannas, responses of [P] and [TP] indicated that large

278 herbivores other than elephants have similar potential. Although our results provided

279 limited support for our hypothesis, the general trends in the results were aligned with

280 predictions and corroborate observations of other studies (du Toit et al., 1990; Ward

281 and Young, 2002).

282   The hypothesis that current season's shoots are shorter in plants after exclusion of

283 large herbivores than in browsed plants in semi-arid savannas was supported for two

284 species we studied. The two fine-leaf, spiny species, *D. cinerea* and *A. grandicornuta*,

285 had shorter shoots after total exclusion compared to either no exclusion or exclusion

286 of elephants. Mean shoot lengths on the two broad-leaf, spineless species were not

287 significantly affected by exclusion, but showed a similar trend. Nevertheless, our

288 results indicated that the study species were able to increase shoot growth rate in

289 response to browsing (Renton et al., 2007; Mopipi et al., 2009) and suggests that

290 spines or N_2-fixation may have a role in compensatory shoot growth, although the

291 mechanism is unclear. The observations for *A. grandicornuta* and *D. cinerea*

292 confirmed preliminary observations of shoot lengths in the previous wet season

293 (ZSKBP, unpublished data). The observations for *C. apiculatum* and *G. flavescens*,

294 however, contrasted with our preliminary observations and other studies that

295 demonstrated shorter shoots without browsing (Bergström et al., 2000) and may have

296 been affected by the specific time of sampling (we suspect that significant effects may

297 have been detected in December when there was a second flush of growth that was

298 more vigorous than the first flush). Unlike the clustered arrangement of leaves at

299 nodes on short-shoots (spurs) in *A. grandicornuta* and *D. cinerea*, leaves on *C.*

apiculatum and *G. flavescens* are produced on long-shoots with one or two leaves per

node (Schmidt et al., 2007). Species with the latter growth pattern cannot produce

new photosynthetic tissues without first producing new somatic tissues, which

requires plenty of water and N (Ganqa and Scogings, 2007). We postulate that

required resources were not sufficient at the time of sampling to meet the

requirements of long-shoot production, leading to the lack of exclusion effect on shoot

length in *C. apiculatum* and *G. flavescens*. Nevertheless, our evidence altogether

indicates that shoot growth rate increases under browsing pressure, which supports

other studies (Fornara and du Toit, 2007; Hrabar et al., 2009).

The decrease in both shoot length and [TP] in *D. cinerea* following exclusion of

large herbivores (the latter contradicting our predictions) suggests that herbivory does

not necessarily result in C limitation in deciduous trees, which supports studies among

boreal species (Nykanen and Koricheva, 2004; Palacio et al., 2008). However,

responses to browsing may be modified by the frequency of browsing, nutrient

availability, the timing of damage and the plant tissue sampled (Hjältén et al., 1993,

1994; Lindroth et al., 2007). Plants accumulate C under nutrient stress (Herms and

Mattson, 1992), which could result in increased levels of CBSMs in browsed plants

(Rooke and Bergstrom, 2007). Alternatively, browsed plants may accumulate C from

compensatory photosynthesis and allocate some of it to increased CBSMs (Medhurst

et al., 2006; Olesen et al., 2008). If sufficient leaves remain after browsing,

photosynthesis contributes more than storage to the allocation of C to growth or

defence (*ibid.*). However, the relative contributions of compensatory photosynthesis

and storage to the increase in both [TP] and shoot growth in *D. cinerea* are unclear.

Dichrostachys cinerea is a fast-growing, aggressive invader that readily produces root

suckers (Tobler et al., 2003; Wakeling and Bond, 2007). In the study area, *D. cinerea*

325   stems grow faster than stems of other species (Scogings, 2011). Carbon allocation

326   patterns in browsed *D. cinerea* are possibly linked to high photosynthetic capacity and

327   extensive storage associated with its growth habit. Given that our plants were not

328   obviously nutrient stressed, compensatory photosynthesis is a likely source of C for

329   allocation to CBSMs in *D. cinerea*, but storage cannot be ignored as a potential source

330   as well. Studies of C allocation in deciduous species in semi-arid savannas would

331   improve the understanding of responses to browsing.

332

333

334   **5. Conclusions**

335

336   In conclusion, effects of browser exclusion on woody plants were species-specific.

337   We found only limited support among the four study species for our prediction that

338   removal of large herbivores results in decreased plant quality (reduced N and

339   increased CBSM) in semi-arid savannas. Furthermore, there was moderate support for

340   our prediction that removal of large herbivores results in decreased shoot length.

341   Therefore, manifestation of positive browse-browser feedback loops in savannas

342   depends on the plant species observed, the specific nutrient or CBSM measured, and

343   the density and composition of the associated herbivore assemblage. Since elephant

344   densities in the study area were high and most positive responses were detected in the

345   control plot, we conclude that elephants probably are important drivers of feedback

346   loops among woody plants taller than 2 m in the study area.

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349   **Acknowledgements**

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362 **References**

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364 Ballare, C.L., 2011. Jasmonate-induced defenses: a tale of intelligence, collaborators

365   and rascals. Trends in Plant Science 16, 249-257.

366 Barton, K.E., Koricheva, J., 2010. The ontogeny of plant defense and herbivory:

367   characterizing general patterns using meta-analysis. American Naturalist 175, 481-

368   493.

369 Bergström, R., Skarpe, C., Danell, K., 2000. Plant response and herbivory following

370   simulated browsing and stem cutting of *Combretum apiculatum*. Journal of

371   Vegetation Science 11: 409-414.

372 Briske, D.D., 1996. Strategies of plant survival in grazed systems. In: Hodgson, J.,

373   Illius, A.W. (Eds.), The Ecology and Management of Grazing Systems. CAB

374   International, Wallingford, pp. 37-67.

375   Bryant, J.P., Chapin, F.S., Reichardt, P., Clausen, T., 1985. Adaptation to resource

376   availability as a determinant of chemical defense strategies in woody plants.

377   Recent Advances in Phytochemistry 19, 219-237.

378   Dangerfield, J.M., Modukanele, B., 1996. Overcompensation by *Acacia erubescens* in

379   response to simulated browsing. Journal of Tropical Ecology 12, 905-908.

380   Du Toit, J.T., Bryant, J.P., Frisby, K., 1990. Regrowth and palatability of *Acacia*

381   shoots following pruning by African savanna browsers. Ecology 71, 149-154.

382   Fornara, D.A., du Toit, J.T., 2007. Browsing lawns? responses of *Acacia nigrescens*

383   to ungulate browsing in an African savanna. Ecology 88, 200-209.

384   Ganqa, N.M., Scogings, P.F. 2007. Forage quality, twig diameter, and growth habit of

385   woody species selected by black rhinoceros in the Great Fish River Reserve, South

386   Africa. Journal of Arid Environments 70, 514-526.

387   Grant, C.C., Scholes, M.C., 2006. The importance of nutrient hotspots in the

388   conservation and management of large wild mammalian herbivores in semi-arid

389   savannas. Biological Conservation 130, 426-437.

390   Grant, C.C., Bengis, R., Balfour, D., Peel, M., 2008. Controlling the distribution of

391   elephants. In: Scholes, R.J., Mennell, K.G. (Eds.), Elephant Management: A

392   Scientific Assessment for South Africa. Wits University Press, Johannesburg, pp.

393   329-369.

394   Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: to grow or defend.

395   Quarterly Review of Biology 67, 283-335.

396   Hester, A.J., Bergman, M., Iason, G.R., Moen, J., 2006. Impacts of large herbivores

397   on plant community structure and dynamics. In: Danell, K., Bergström, R.,

398   Duncan, P., Pastor, J. (Eds.), Large Herbivore Ecology, Ecosystem Dynamics and

399   Conservation. Cambridge University Press, Cambridge, pp. 97-141.

400   Hjältén, J., Danell, K., Ericson, L., 1993. Effects of simulated herbivory and

401   intraspecific competition on the compensatory ability of birches. Ecology 74,

402   1136-1142.

403   Hjältén, J., Danell, K., Ericson, L., 1994. The impact of herbivory and competition on

404   the phenolic concentration and palatability of juvenile birches. Oikos 71, 416-422.

405   Hjältén, J., Danell, K., Ericson, L., 1996. Food selection by two vole species in

406   relation to plant growth strategies and plant chemistry. Oikos 76, 181-190.

407   Hrabar, H., Hattas, D., du Toit, J.T., 2009. Differential effects of defoliation by

408   mopane caterpillars and pruning by African elephants on the regrowth of

409   *Colophospermum mopane* foliage. Journal of Tropical Ecology 25, 301-309.

410   Jonsson, M., Bell, D., Hjältén, J., Rooke, T., Scogings, P.F., 2010. Do mammalian

411   herbivores influence invertebrate communities via changes in the vegetation?

412   Results from a preliminary survey in Kruger National Park, South Africa. African

413   Journal of Range and Forage Science 27, 39-44.

414   Khomo, L.M., Rogers, K.H., 2005. Proposed mechanism for the origin of sodic

415   patches in Kruger National Park, South Africa. African Journal of Ecology 43, 29-

416   34.

417   Koricheva, J., Larsson, S., Haukioja, E., Keinanen, M., 1998. Regulation of woody

418   plant secondary metabolism by resource availability: hypothesis testing by means

419   of meta-analysis. Oikos 83, 212-226.

420   Levick, S., Rogers, K.H., 2008. Patch and species specific responses of savanna

421   woody vegetation to browser exclusion. Biological Conservation 141, 489-498.

422   Lindroth, R.L., Donaldson, J.R., Stevens, M.T., Gusse, A.C. 2007. Browse quality in

423   quaking aspen (*Populus tremuloides*): Effects of genotype, nutrients, defoliation,

424   and coppicing. Journal of Chemical Ecology 33, 1049-1064.

425 Medhurst, J.L., Pinkard, E.A., Beadle, C.L., Worledge, D., 2006. Photosynthetic

426   capacity increases in *Acacia melanoxylon* following form pruning in a two-species

427   plantation. Forest Ecology and Management 233, 250-259.

428 Milton, S.J., 1988. The effects of pruning on shoot production and basal increment of

429   *Acacia tortilis*. South African Journal of Botany 54, 109-117.

430 Mopipi, K., Trollope, W.S.W., Scogings, P.F., 2009. Effects of moisture, nitrogen,

431   grass competition and simulated browsing on the survival and growth of *Acacia*

432   *karroo* seedlings. African Journal of Ecology 47, 680-687.

433 Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination

434   of phosphate in natural ecosystems. Analytica Chimica Acta 27, 31-36.

435 Nykanen, H., Koricheva, J., 2004. Damage-induced changes in woody plants and their

436   effects on insect herbivore performance: a meta-analysis. Oikos 104, 247-268.

437 O'Keefe, T., Alard, G., 2002. Effects of Herbivores and Fire on Riparian and Upland

438   Savanna Ecosystems: Field Operations Manual for Herbivore and Fire Exclosures

439   on the Sabie and Letaba Rivers in the Kruger National Park. SANParks, Skukuza.

440 Olesen, T., Robertson, D., Muldoon, S., Meyer, R., 2008. The role of carbohydrate

441   reserves in evergreen tree development, with particular reference to macadamia.

442   Scientia Horticultura. 117, 73-77.

443 Orians, C.M., Thorn, A., Gomez, S., 2011. Herbivore-induced resource sequestration

444   in plants: why bother? Oecologia 167, 1-9.

445 Palacio, S., Hester, A.J., Maestro, M., Millard, P., 2008. Browsed *Betula pubescens*

446   trees are not carbon-limited. Functional Ecology 22, 808-815.

447 Porter, L.J., Hrstich, L.N., Chan, B.C., 1986. The conversion of procyanidins and

448   prodelphinidins to cyanidin and delphinidin. Phytochemistry 25, 223-230.

449   Price, M.L., Butler, L.G., 1977. Rapid visual estimation and spectrophotometric

450   determination of tannin content of sorghum grain. Journal of Agricultural and

451   Food Chemistry 25, 1268-1273.

452   Renton, M., Thornby, D., Hanan, J., 2007. Canonical modelling: an approach for

453   intermediate-level simulation of carbon allocation in functional-structural plant

454   models. In: Vos, J., Marcelis, L., de Visser, P., Struik, P.C., Evers, J.B. (Eds.),

455   Functional-structural Plant Modelling in Crop Production. Springer, Dordrecht,

456   pp. 151-164.

457   Rooke, T., Bergstrom, R., 2007. Growth, chemical responses and herbivory after

458   simulated leaf browsing in *Combretum apiculatum*. Plant Ecology 189, 201-212.

459   Schmidt, E., Lötter, M., McCleland, W., 2007. Trees and Shrubs of Mpumalanga and

460   Kruger National Park. Jacana Media, Johannesburg.

461   Scogings, P.F., 2011. Stem growth of woody species at the Nkuhlu Exclosures,

462   Kruger National Park: 2006-2010. Koedoe 53, doi:10.4102/koedoe.v53i1.1035.

463   Siebert, F., Eckhardt, H.C., 2008. The vegetation and floristics of the Nkuhlu

464   exclosures, Kruger National Park. Koedoe 50, 126-144.

465   Skarpe, C., Hester, A.J., 2008. Plant traits, browsing and grazing herbivores, and

466   vegetation dynamics. In: Gordon, I.J., Prins, H.H.T. (Eds.), The Ecology of

467   Browsing and Grazing. Springer, Berlin, pp. 217-261.

468   Skinner, J.D., Chimimba, C.T., 2005. The mammals of the southern African

469   subregion. Cambridge University Press, Cape Town.

470   Stevens, M.T., Waller, D.M., Lindroth, R.L., 2007. Resistance and tolerance in

471   *Populus tremuloides*: genetic variation, costs, and environmental dependency.

472   Evolutionary Ecology 21, 829-847.

473   Tarasoff, C.S., Mallory-Smith, C.A., Ball, D.A., 2007. Comparative plant responses

474   of *Puccinellia distans* and *Puccinellia nuttalliana* to sodic versus normal soil

475   types. Journal of Arid Environments 70, 403-417.

476   Teague, W.R., 1985. Leaf growth of *Acacia karroo* trees in response to frequency and

477   intensity of defoliation. In: Tothill, J.C., Mott, J.J. (Eds). Ecology and

478   Management of the World's Savannas. Australian Academy of Science, Canberra,

479   and CAB, Farnham Royal, pp. 220-222.

480   Teague, W.R., Walker, B.H., 1988. Effect of intensity of defoliation by goats at

481   different phenophases on leaf and shoot growth of *Acacia karroo* Hayne. Journal

482   of the Grassland Society of Southern Africa 5, 197-206.

483   Tobler, M.W., Cochard, R., Edwards, P.J., 2003. The impact of cattle ranching on

484   large-scale vegetation patterns in a coastal savanna in Tanzania. Journal of

485   Applied Ecology 40, 430-444.

486   Underwood, A.J., 1997. Experiments in Ecology. Cambridge University Press,

487   Cambridge.

488   Wakeling, J.L., Bond, W.J., 2007. Disturbance and the frequency of root suckering in

489   an invasive savanna shrub, *Dichrostachys cinerea*. African Journal of Range and

490   Forage Science 24, 73-76.

491   Ward, D., Young, T.P., 2002. Effects of large mammalian herbivores and ant

492   symbionts on condensed tannins of *Acacia drepanolobium* in Kenya. Journal of

493   Chemical Ecology 28, 913-929.

494   Williams, C.A., Hanan, N., Scholes, R.J., Kutsch, W., 2009. Complexity in water and

495   carbon dioxide fluxes following rain pulses in an African savanna. Oecologia 161,

496   469-480.

497

Figure legends

499

500 **Fig. 1.** Mean concentrations of N and P (mg/g), and total polyphenols (TP, mg gallic

501 acid equivalents/g) and condensed tannins (CT, mg sorghum tannin equivalents/g) in

502 mature leaves from four species (Ag = *A. grandicornuta*, Ca = *C. apiculatum*, Dc = *D.*

503 *cinerea*, Gf = *G. flavescens*) at Nkuhlu, 28-30 January 2008. Letters above columns

504 indicate significant differences among means within species, according to Bonferroni

505 means comparison ($P < 0.05$). Error bars are standard errors of means (n = 15-18, 14-

506 18, 16-18 and 10-16 for Ag, Ca, Dc and Gf, respectively).

507

508 **Fig. 2.** Mean length (cm) of unbrowsed new shoots at 1.5-2.5 m on *A. grandicornuta*,

509 *C. apiculatum* and *D. cinerea*, and above 1 m on *G. flavescens*, at Nkuhlu (November

510 2007). Ten shoots were averaged per tree. Error bars are standard errors of means.

511 Letters above columns indicate significant differences among means within species

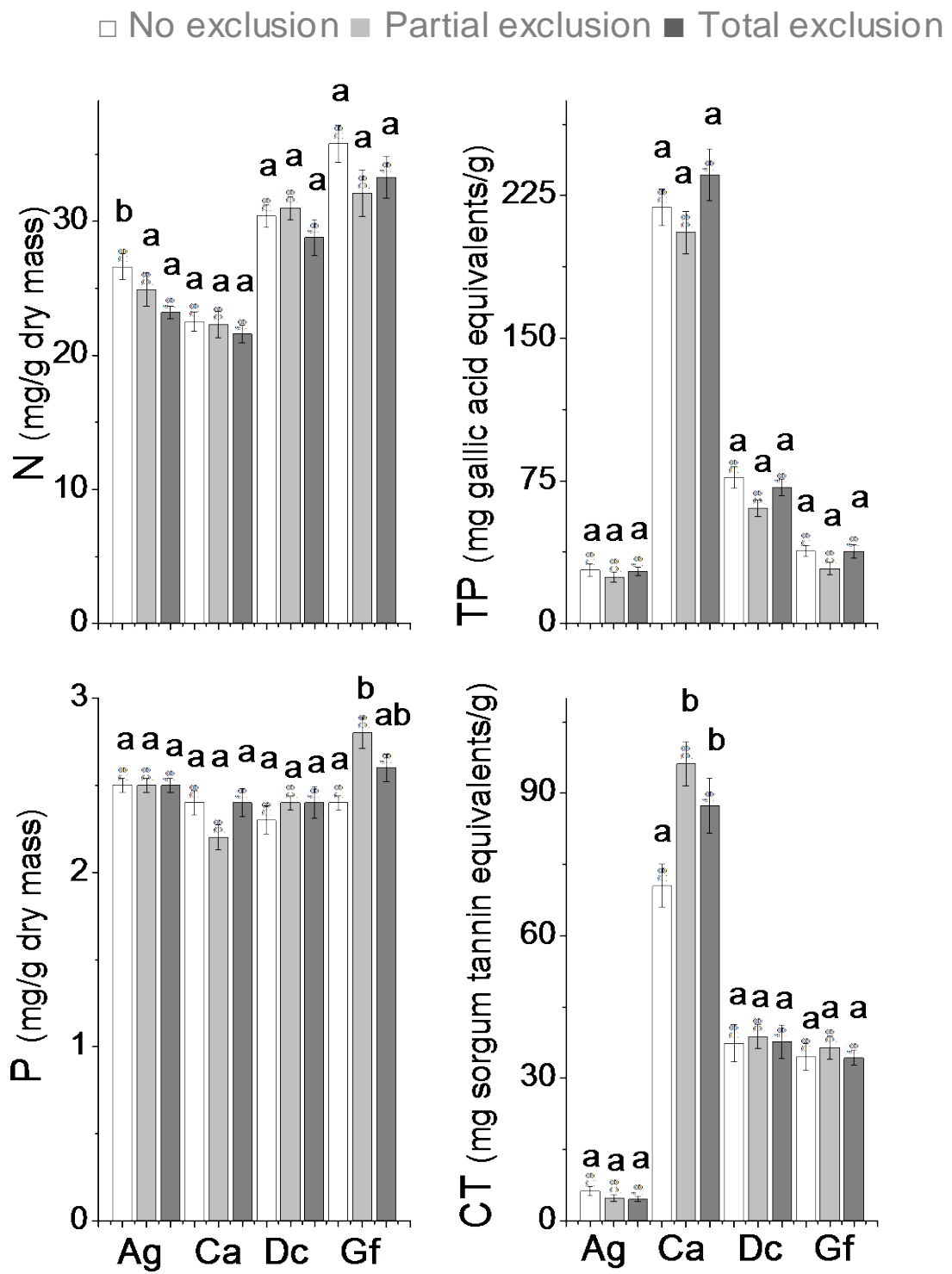512 according to Bonferroni means comparison ($P < 0.05$; n = 5).

Figure 1

Figure 2