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2 **independently affected by large herbivores and shoot growth rate**

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38   **Abstract** Carbon-based secondary metabolites (CBSMs) such as tannins are assumed

39   to function as plant defences against herbivores. CBSMs are thought to be inversely

40   related to growth rate and nutrient concentrations because a physiological trade-off

41   exists between cellular growth and differentiation, but CBSM concentrations can be

42   altered by herbivory-induced changes in the trade-off. We predicted that a significant

43   interaction exists between herbivory and growth phase, such that the effects of large

44   herbivores (or their exclusion) on nutrient or CBSM concentrations are greatest during

45   phases of rapid shoot or leaf growth. Leaf samples were collected during phases of

46   different growth rate from six woody species four years after establishment of a large-

47   scale long-term herbivore exclusion experiment in Kruger National Park, South Africa.

48   Samples were analysed for N, P, condensed tannins and total phenolics. Interactions

49   between growth phase and herbivores were rare. However, the assumption that elevated

50   nutrients and reduced CBSMs occur during fast phases of growth was supported by four

species (consistent with the growth-differentiation balance hypothesis), but not the other two. Large herbivores generally did not affect nutrients, but CBSMs in four species were reduced by large herbivores other than elephants, while CBSMs in two species were reduced by elephants. Carbon limitation ultimately prevailed among woody plants taller than 2 m under long-term browsing. Large herbivores and plant growth phase are independent and important determinants of nutrients or CBSMs in African savannas, but the effects depend on the interacting assemblages of species, which poses challenges to the application of current general hypotheses of plant defence.

Key words Elephant, Exclusion experiment, Herbivore, Phenology, Plant defence

Introduction

Plant-herbivore interactions have profound impacts on ecosystems (Pastor et al. 2006). On the plant scale, several traits affect herbivore food choice, such as plant secondary metabolite and nutrient concentrations, which affect digestibility (Skarpe and Hester 2008). Carbon-based secondary metabolites (CBSMs), such as tannins and phenols, are ecologically important because they are assumed to function as chemical defences that contribute to the herbivore-avoidance strategies of woody plants (Skarpe and Hester 2008; Barbehenn and Constabel 2011; Boeckler et al. 2011). Nutrients, such as N and P, contribute to a plant's overall value for herbivores (Mårell et al. 2005). However, these plant traits do not only vary among plant species, but also vary over time and in response to herbivory (Lindroth et al. 2007). Models that explain variations in CBSMs

76 predict that growth rate and nutrient concentration are inversely related to CBSM

77 concentrations because a physiological trade-off exists between cellular growth and

78 differentiation processes (Herms and Mattson 1992; le Bot et al. 2009). Furthermore,

79 plants respond to herbivores by adjusting growth rate and, consequently, CBSM and

80 nutrient concentrations (Skarpe and Hester 2008). While defoliation may induce

81 defences in woody plants (Ward and Young 2002; Wessels et al. 2007), severe

82 browsing (especially when twig biting is involved) has been reported to have the

83 opposite effect by causing either increased N concentrations or reduced tannin

84 concentrations in individual plants (du Toit et al. 1990; Danell et al. 2003; Persson et al.

85 2005). A browsing-induced switch to a vegetative state characterised by fast-growing,

86 N-rich/C-poor tissues potentially increases a plant's risk of being browsed again

87 (Fornara and du Toit 2007; Skarpe and Hester 2008). One explanation given for the

88 positive feedback is preferential allocation of C to growth of new shoots rather than

89 CBSMs (Fornara and du Toit 2007; Hrabar et al. 2009), which can be achieved when

90 the root:shoot ratio is altered such that shoot growth increases to restore the ratio

91 (Herms and Mattson 1992; Renton et al. 2007).

92   The responses of individual plants to years or decades of accumulated losses to

93 browsing are not clearly predicted by current models of herbivore resistance. Browse-

94 browser interactions are particularly relevant in Africa because of the abundance of

95 large herbivores compared to other continents (Bond et al. 2001; Fritz and Loison

96 2006). Therefore, a critical component of research in African savannas is the effects that

97 large herbivores have on woody plants, with the ultimate objective being the

98 development of improved management policies (O'Keefe and Alard 2002). While

99 numerous studies have measured browsing induced changes in either growth or CBSMs

100 in savannas, few have considered the responses of both growth and CBSMs

101   simultaneously (Scogings et al. 2013b). Most of the latter studies have been short-term

102   experiments using manual methods of simulated browsing applied to deciduous species.

103   The majority of these studies have shown increased shoot growth and unchanged CBSM

104   concentrations in response to browsing (Gowda 1997; Gadd et al. 2001; Katjiua and

105   Ward 2006; Hrabar et al. 2009), but some have found increased shoot growth and either

106   increased or decreased CBSM concentrations (Scogings and Macanda 2005; Rooke and

107   Bergström 2007). The studies that considered both growth and nutrients or CBSMs

108   under long-term browsing are equally inconclusive. They showed either decreased shoot

109   or leaf growth with no change in CBSM concentrations (Zinn et al. 2007), or increased

110   shoot growth with either unchanged CBSM concentrations, or increased nutrient

111   concentrations coupled with decreased CBSM concentrations (Fornara and du Toit

112   2007, Hrabar et al. 2009). There is a need for further research into the effects of

113   browsing on nutrient or CBSM concentrations among woody species in African

114   savannas, which would contribute to determining the utility of models based on growth-

115   differentiation trade-offs for understanding plant-herbivore dynamics in savannas.

116   The main aim of this paper was to determine how concentrations of foliar

117   nutrients or CBSMs of woody species are affected by large herbivores and different

118   phases of shoot / leaf growth in a semi-arid savanna. Savannas are characterised by

119   alternating wet and dry seasons that are each several months long (Kutsch et al. 2008).

120   Most subtropical savannas in Africa are semi-arid and water is the main limiting

121   resource for plant growth for most of the year (Scholes et al. 2003; Jacobs et al. 2007).

122   Nitrogen is most available early in the wet season when elevated soil water drives

123   mineralization (Scholes et al. 2003). Shoot growth therefore occurs in brief phases

124   during the wet season (Williams et al. 2009). Our primary underlying assumption was

125   that changes in shoot / leaf growth rate during the wet season lead directly to differences

126   in foliar concentrations of nutrients or CBSMs (rather than foliar chemistry being

127   directly affected by nutrient or water availability). We specifically assumed that during

128   phases of fast shoot or leaf growth nutrient concentrations are highest, or CBSM

129   concentrations are lowest, because of a trade-off between cellular growth and

130   differentiation (Herms and Mattson 1992; Martz et al. 2010). We also explicitly

131   assumed that browsing is capable of inducing defences (e.g., increase tannin

132   concentrations) when CBSM concentrations are low and growth rate is high (Bryant et

133   al. 1991; Scogings et al. 2011). We therefore hypothesised a significant interaction

134   between browsing and growth phase, such that the effects of browsers on nutrient or

135   CBSM concentrations are greatest during phases of rapid shoot or leaf growth. We

136   tested our hypothesis by sampling six woody species during different growth phases in

137   one wet season in a large-scale, long-term exclusion experiment in Kruger National

138   Park, South Africa. The species were among the most abundant in the study area and are

139   common elsewhere (Online Resource 1). Inclusion of several, commonly occurring

140   species in the study enriched the study by providing an opportunity for species-specific

141   responses to be discovered (Levick and Rogers 2008). In addition, the design of the

142   exclusion experiment encouraged exploration of the roles of different assemblages of

143   large herbivores (Jonsson et al. 2010). The landscape scale of our approach is useful for

144   the management of extensive areas used for either biodiversity conservation or livestock

145   production (Levick and Rogers 2008).

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148   **Materials and methods**

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150   Sampling

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Experimental exclusion treatments (24° 58′ S, 31° 46′ E) were established adjacent to

the Sabie River, Kruger National Park, South Africa in 2002 on the premise that

exclusion of large herbivores (especially elephants) would allow their effects to be

determined (O'Keefe and Alard 2002). Treatments could not be replicated because of

the large scale needed for informing management decisions in extensive conservation

areas comprising heterogeneous landscapes and mega-herbivores (Levick and Rogers

2008; Jonsson et al. 2010). One exclusion treatment excludes all herbivores the size of

hares and larger (total exclusion; 70 ha), while a second exclusion treatment excludes

elephants, but not other herbivores (partial exclusion; 44 ha). Although exclusion of

giraffe from the partial exclusion treatment is unavoidable, they are not as abundant as

elephants in the study area and their effect is assumed to be negligible. The two

exclusion treatments are separated by a control area open to all large herbivores (no

exclusion; 25 ha). Therefore, if allowing elephants has any additional effects on

vegetation than allowing only other large herbivores, then it can be inferred that

elephants are the main source of the differences between exclusion and control

treatments (Jonsson et al. 2010). If excluding elephants shows a different response than

excluding all large herbivores then it can be inferred that other wildlife are a source of

the differences between exclusion and control treatments.

Crests and midslopes in the treatments are characterized by shallow, sandy,

coarse soil, while footslopes are characterized by deep, sodic, duplex soil (Khomo and

Rogers 2005; Grant and Scholes 2006). We sampled five deciduous and one evergreen

species during the 2006/2007 wet season. The selected species were among the most

abundant in the study area and included *Acacia grandicornuta* and *Euclea divinorum* on

the footslopes and *Dichrostachys cinerea*, *Acacia exuvialis*, *Combretum apiculatum* and

176 *Grewia flavescens* on the middle slopes and crests (see Online Resource 1 for details of

177 study area and species). Methods for measuring shoot or leaf growth were species-

178 specific because of differences in shoot morphology. Both *D. cinerea* and the two

179 *Acacia* species produce most of their new leaves in discrete clusters of leaves at nodes

180 on old shoots or branches and therefore increase leaf area without growing internodes.

181 Conversely, *C. apiculatum*, *G. flavescens* and *E. divinorum* produce all their new leaves

182 on new shoots and therefore cannot increase leaf area without extending new internodes

183 (Scogings et al. 2013a). The latter species experience more browsing by shoot biting

184 than leaf nibbling and therefore experience more loss of biomass due to browsing

185 compared to other species (Bond et al. 2001; Scogings et al. 2011).

186   Up to 10 new shoots and 10 new leaves on new shoots were selected on each of

187 five trees per species in each exclusion treatment during the third week of November

188 (two weeks after the first rainfall). Catenal position could not be regarded as a treatment

189 because no species occurred across the catena. A 30 x 30 m grid was used to randomly

190 locate plants. One tree of each study species was sampled in each of 10 randomly

191 selected grid cells (five for the species inhabiting crests / midslopes and five for the

192 species on footslopes) per treatment on condition that it was (1) closest to the grid-cell

193 centre, (2) taller than 2 m (1.5 m for *G. flavescens* because it seldom grows taller than 2

194 m), and (3) neither obviously stressed by disease, disturbance or neighbours nor

195 obviously growing in a nutrient enriched patch. If any of the conditions failed to be met

196 for the closest tree, then the next closest tree that met the conditions was sampled. No

197 tree was sampled if the closest suitable tree was further than 15 m from the grid-cell

198 centre to avoid infringement of neighbouring cells. A similar study of trees shorter than

199 2 m was conducted in a different year (Scogings et al. 2013b).

200   The new shoots were selected by locating 10 old shoots (from a previous wet

201   season) per tree. Each old shoot was 2-8 mm in basal diameter and 1.5-2.5 m above

202   ground (>1 m for *G. flavescens*). Old shoots were marked by loosely twisting short

203   pieces of thin, plastic-coated wire around the shoot base. Unique colour combinations

204   were used to differentiate individual shoots. The most distal new shoot on each old

205   shoot was then marked by painting a small spot of white "correction fluid" (Tippex®) at

206   the base. In addition to marking new shoots on *A. exuvialis, A. grandicornuta* and *D.*

207   *cinerea*, which had very few new shoots, one leaf cluster was marked on each marked

208   old shoot. The leaf cluster with the longest leaf was marked with a small spot of

209   Tippex® painted on the old shoot. The length of each marked new shoot was measured

210   (nearest 0.1 cm) from the base of the shoot to the base of the apical bud. The length of

211   the longest leaf on each marked new shoot and in each marked leaf cluster was

212   measured (nearest 0.1 mm) from the base of the petiole to the apex of the midrib

213   (simple leaves) or rachis (compound leaves). Each marked shoot that still had an intact

214   apical bud in the first week of December, last week of January and last week of March

215   was re-measured. The longest leaf on each marked shoot and in each marked leaf cluster

216   was also re-measured.

217   Around each time that shoots and leaves were measured, six other plants of each

218   species were located in each treatment by randomly selecting grid cells as described

219   above. Leaf samples were collected from each plant by clipping branches 3-8 mm in

220   diameter from the northern, sunlit half of the canopy between 1.5 and 2.2 m above

221   ground, which was within the range of most browsers in the study area. For *G.*

222   *flavescens*, the lowest permissible height for collection was reduced to 1.0 m because of

223   its low stature. Branches were collected 1-4 hours after sunrise. Leaves that did not

224   show signs of severe insect herbivory were randomly removed until a fresh mass of 30-

225   50 g was obtained for drying in an oven for 24 hours at 60 °C. Dried leaf samples were

226   milled to pass a sieve with 1.0 mm apertures and were analysed for concentrations of

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

228   1977), Kjeldahl-N ([N]) (AOAC 1990) and phosphorus ([P]) (Murphy and Riley 1962).

229   All concentrations were expressed in mg g^{-1} dry mass. [CT] and [TP] were expressed as

230   *Sorghum* tannin equivalents (STE) and Gallic acid equivalents (GAE), respectively. We

231   note that variations detected by the CBSM assays may have several explanations,

232   including changes in composition and reactivity.

233

234   Data analysis

235

236   Data were analysed separately for each species because we expected responses to be

237   species-specific (Scogings et al. 2011). Trees were replicates. Therefore, pseudo-

238   replication constrained the analysis (Underwood 1997). The shoot and leaf length data

239   were averaged per tree, after which mean shoot or leaf length and associated standard

240   error ($n = 5$) were plotted against time to identify distinct phases of growth (fast or

241   slow). Chemical data were transformed to $\log_{10}(x)$, or $\log_{10}(\log_{10}(x))$, when this

242   normalised the data. The ANOVA model containing the effects of herbivores (three

243   levels), growth phase (two levels), and their interaction, was tested for [N], [P], [TP]

244   and [CT] of each species, assuming a completely randomised design and type III sums

245   of squares for unequal sample sizes. Tukey's HSD test was used to separate the means.

246   Significance was declared when $P < 0.05$, while noteworthy trends were not ignored

247   when $0.10 > P > 0.05$ (Underwood 1997).

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249

250   **Results**

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252   Two distinct phases of shoot or leaf growth were obvious, being rapid growth during the

253   first 4-5 weeks of the wet season, followed by slow or negligible growth for the rest of

254   the wet season in the deciduous species while the reverse pattern was observed in the

255   evergreen species (Online Resource 2). Notwithstanding effects of growth phase and

256   herbivores, species varied substantially in terms of measured chemical variables (Fig.

257   1). The only significant interaction between growth phase and exclusion treatment,

258   suggesting that herbivore influence on plant chemistry differed between seasons, was

259   for [CT] in *E. divinorum* (Fig. 2, Online Resource 3). While [CT] in *E. divinorum* was

260   generally higher in the slow than the fast growth phase, it was lowest in the fast growth

261   phase when large herbivores were present (Fig. 2). Marginally significant interactions

262   were noted for both [CT] and [TP] in *A. grandicornuta* (Online Resource 3), suggesting

263   that elephants tended to reduce [CT] and [TP] during the slow growth phase (Fig. 2).

264   Across all species, growth phase consistently affected both [N] and [P], which

265   were lowest during the phase of slow growth, except in *E. divinorum* where the opposite

266   was observed (Fig. 1, Online Resource 3). In *A. exuvialis* and *D. cinerea* [TP] was not

267   significantly affected by growth phase (Fig. 1, Online Resource 3). In contrast, [TP] in

268   *G. flavescens* and *E. divinorum* was higher during the slow than the fast growth phase,

269   but the opposite was observed in *A. grandicornuta* and *C. apiculatum* (Fig. 1, Online

270   Resource 3). In *A. exuvialis*, *D. cinerea*, *C. apiculatum* and *G. flavescens* [CT] was

271   higher during the slow than the fast growth phase, but the opposite was observed in *A.*

272   *grandicornuta* (Fig. 1, Online Resource 3).

273   Herbivores significantly affected [P] in *A. exuvialis* (Table 1), which was lower

274   (mean = 2.35 mg g^{-1}; SEM = 0.090; *n* = 23) where all large herbivores were excluded,

275   compared to where either all large herbivores were present (mean = 2.76 mg g^{-1}; SEM =

276   0.151; *n* = 24) or all large herbivores except elephants were present (mean = 2.62 mg g^{-1}

277   ; SEM = 0.129; *n* = 22). In both *A. exuvialis* and *D. cinerea* [TP] was not significantly

278   affected by herbivores (Online Resource 3). However, in both *C. apiculatum* and *G.*

279   *flavescens*, [TP] was highest when all large herbivores were excluded, but in *E.*

280   *divinorum* [TP] was higher when elephants were excluded than when no herbivores

281   were excluded (Figs 2-3, Online Resource 3). In both *A. exuvialis* and *C. apiculatum*

282   [CT] was highest when all large herbivores were excluded (Fig 3, Online Resource 3).

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284

285   **Discussion**

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287   One of our assumptions was that nutrient concentrations are highest, or CBSM

288   concentrations are lowest, during phases of fast shoot or leaf growth. The higher

289   nutrient concentrations and lower [CT] during the fast growth phase compared to the

290   slow growth phase, except for *E. divinorum* and *A. grandicornuta*, supported the

291   growth-differentiation balance hypothesis (GDBH) of plant defence (Herms and

292   Mattson 1992). However, [TP] in only two species (*G. flavescens* and *E. divinorum*)

293   supported the GDBH by being lowest during the fast growth phase. Thus, some

294   paradoxes were clear: (i) high [N] and [P] in the slow growth phase in *E. divinorum*, (ii)

295   high or unchanged [TP] in the fast growth phase in four species, and (iii) high [CT] in

296   the fast growth phase in *A. grandicornuta*. An explanation for reduced nutrient

297   concentrations during the fast growth phase of *E. divinorum* late in the wet season is

298   that evergreen species are known to withdraw nutrients from leaves to supply new

299   apical buds (Pallardy 2008; Pornon et al. 2011). The ability of *E. divinorum* to grow late

300   in the wet season appears to be related to its occurrence on footslopes. A substantial

301   proportion of rainfall infiltrates the coarse sandy soil on crests and eventually

302   accumulates in the deep clay-rich subsoil of footslopes late in the wet season (Jacobs et

303   al. 2007). The difference in the timing of water availability across the catena also

304   supports observations that both *E. divinorum* and *A. grandicornuta* maintain positive

305   radial stem growth in the dry season, while species on the sandy crests do not (Scogings

306   2011). Further evidence of increased water availability in footslope soils is the ability of

307   *A. grandicornuta* to retain green leaves through most of the dry season in some years,

308   despite being generally deciduous (Zululand/Sweden Kruger Browse Project,

309   unpublished data). From our results we can infer that footslope species become

310   potentially more palatable (increased N, reduced CT) as the wet season progresses,

311   rather than becoming less palatable. Therefore, we postulate that footslope species are

312   most likely to be eaten late in the season when high resource (water) availability on the

313   footslopes would provide optimal conditions for plant recovery. Conversely, we would

314   expect browsing to be concentrated on the crests early in the wet season when crest

315   species are in optimal conditions to recover. However, support for the above hypothesis

316   is absent and further research is needed.

317   High or unchanged [TP] or high [CT] during phases of fast shoot or leaf growth

318   suggest that some deciduous woody species in savannas are less prone to C limitation

319   than others, which is supportive of other studies (Palacio et al. 2008). Our observations

320   imply either high C storage or high C assimilation capacities among deciduous species,

321   which could be readily achieved in environments where light is not limiting (Scholes et

322   al. 2003; Jolly and Running 2004). Positive associations between CBSM concentrations

323   and growth occur when N is limited enough to affect growth rate but not

324   photosynthesis, i.e., at moderate-high N limitation (Herms and Mattson 1992; Pizarro

325 and Bisigato 2010). We found high CBSM concentrations and fast growth at the start of

326 the wet season, when N is most available (Scholes et al. 2003), suggesting that woody

327 plants in the study area seldom experience high N availability. Therefore, high C

328 reserves are important for woody plants in these ecosystems (Higgins et al. 2000;

329 Scogings et al. 2011). Only *G. flavescens* consistently had high nutrient concentrations

330 and low CBSM concentrations in the fast growth phase, suggesting it was not as N

331 limited as the other species. Furthermore, CBSM synthesis requires N and any increase

332 in N availability can lead to increases in both growth rate and C-based secondary

333 metabolism (le Bot et al. 2009). For example, both *A. grandicornuta* and *D. cinerea* had

334 high CBSM concentrations during the fast growth phase, which may be attributed to N_2-

335 fixation.

336   Our second assumption was that when CBSM concentrations are low and

337 resource availability is high, then CBSM concentrations are increased by browsing. The

338 CBSM concentrations of the species characteristic of the crests and midslopes were

339 reduced by large herbivores such that we inferred that elephants were not the main

340 source of the effect. In contrast, the responses of the species characteristic of footslopes

341 (discussed above) suggested the possibility that CBSMs were sometimes reduced by

342 elephants. Nevertheless, our results corroborated the view that long-term browsing can

343 maintain woody species in positive feedback loops characterised by N-rich or C-poor

344 tissues (Fornara and du Toit 2007; Skarpe and Hester 2008). While long-term browsing

345 generally reduced CBSMs, indicating C limitation among browsed woody plants in the

346 study area, most of the woody species were generally able to accumulate CBSMs during

347 phases of slow shoot or leaf growth during the wet season, indicating an absence of C

348 limitation. We postulate that the reduction of CBSMs under browsing is a result of C

349 being allocated to stimulated shoot or leaf growth (early in the wet season for most

350 species) (Fornara and du Toit 2007), but the increase in CBSMs during slow growth

351 phases (late in the wet season for most species) is a result of C being allocated to

352 functions other than the production of somatic or photosynthetic cells, such as the

353 production of storage, transport, reproductive or defensive cells (Pallardy 2008).

354 However, given that the negative effect of browsing on CBSMs persisted, C limitation

355 ultimately prevailed among woody plants >2 m in height under long-term browsing in

356 the study area.

357   The hypothesis that effects of large herbivores on nutrient or CBSM

358 concentrations would be greater during phases of rapid shoot or leaf growth than during

359 phases of slow growth was not supported. A significant interaction was only observed

360 for [CT] in *E. divinorum*, which during the fast growth phase was most affected by

361 elephant exclusion and therefore supported the hypothesis. *Euclea divinorum* was

362 abundant on footslopes adjacent to a perennial river and experienced high rates of

363 severe damage by elephants, such as branch/stem breakage (Scogings et al. 2012). Use

364 of footslope vegetation increases when elephants increase the time they spend along

365 perennial rivers during periods when other sources of drinking water are scarce (Grant

366 et al. 2008). Rainfall during the 2006/2007 wet season was below the long-term mean

367 (Scogings 2011), suggesting that elephant abundance and impact on the footslopes was

368 intensified, which may have led to reduced defences resulting from C exhaustion (du

369 Toit et al. 1990; Scogings et al. 2011). However, interactions between long-term and

370 short-term effects require further research. Both the observed interaction in *E.*

371 *divinorum* and the tendency for interactions in *A. grandicornuta* suggest that the effects

372 of elephants on these footslope species are greatest late in the wet season. Conversely,

373 we would postulate that the absence of significant interactions among the remaining

374   four species, which were abundant on the crests, was because browsing there was not as

375   intense as on the footslopes (Engdahl 2008).

376

377

378   **Conclusions**

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380   Our observations suggest that plant responses to resource availability (indicated by

381   growth phase) and large herbivores in semi-arid African savannas are additive, rather

382   than multiplicative. Elevated nutrients and reduced CBSMs generally occurred during

383   phases of fast shoot or leaf growth among species characteristic of crests and midslopes,

384   while species characteristic of footslopes responded conversely. In general, large

385   herbivores reduced CBSMs, but did not affect nutrients. Overall, CBSMs in species on

386   crests and midslopes were reduced by large herbivores other than elephants, while

387   CBSMs in species on footslopes were reduced by elephants. Our conclusions should be

388   considered with caution because spatial replication of treatments was not possible.

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Figure legends

Fig. 1 Mean concentrations of nitrogen (mg g^{-1}), phosphorus (mg g^{-1}), total phenolics

(mg Gallic acid equivalents g^{-1}) and condensed tannins (mg *Sorghum* tannin equivalents

g^{-1}) in mature leaves of *Acacia exuvialis* (AE), *Acacia grandicornuta* (AG),

Dichrostachys cinerea (DC), *Combretum apiculatum* (CA), *Grewia flavescens* (GF) and

Euclea divinorum (ED) plants ($n = 36$) at Nkuhlu, Kruger National Park, during fast and

slow growth phases in the 2006/2007 wet season. Leaves were sampled between 1.5 and

2.2 m (1.0 − 1.5 m on *G. flavescens*). Asterisks indicate growth phases with

significantly higher values ($P < 0.05$). Error bars are standard errors of the means

Fig. 2 Effects of large herbivores on mean concentrations of condensed tannins (mg

Sorghum tannin equivalents g^{-1}) and total phenolics (mg Gallic acid equivalents g^{-1}) in

mature leaves between 1.5 and 2.2 m on *Euclea divinorum* and *Acacia grandicornuta* at

Nkuhlu, Kruger National Park ($n = 12$, but $n = 24$ for *E divinorum* total phenolics).

Letters indicate significant differences ($P < 0.05$) between treatments ($P < 0.10$ for *A.*

grandicornuta). Error bars are standard errors of the means

Fig. 3 Effects of large herbivores on mean concentrations of total phenolics (mg Gallic

acid equivalents g^{-1}) and condensed tannins (mg *Sorghum* tannin equivalents g^{-1}) in

mature leaves between 1.5 and 2.2 m on *Acacia exuvialis* and *Combretum apiculatum*,

and between 1.0 and 1.5 m on *Grewia flavescens*, at Nkuhlu, Kruger National Park ($n =$

24). Letters indicate significant differences ($P < 0.05$) between treatments. Error bars
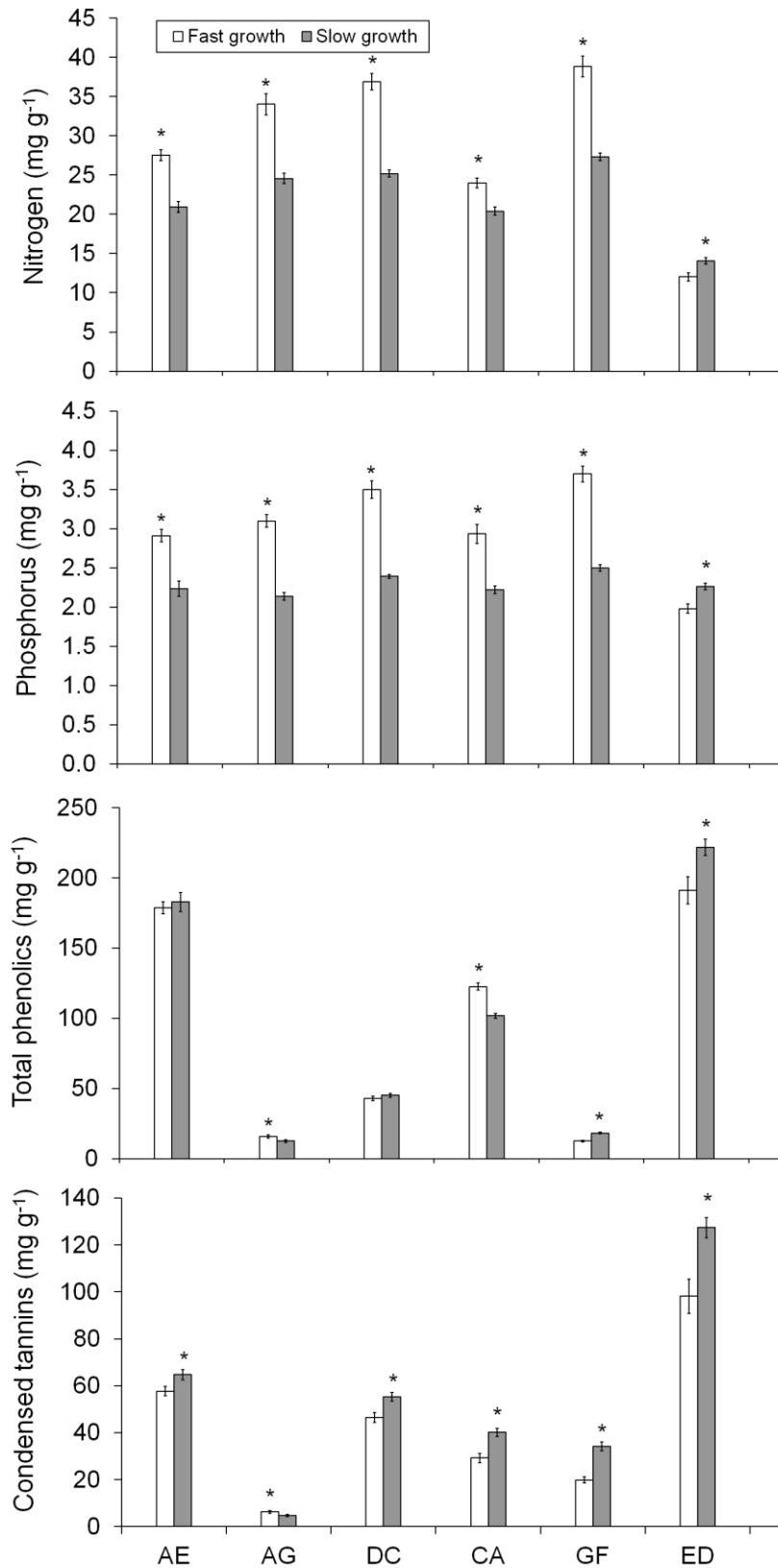
are standard errors of the means

Fig. 1

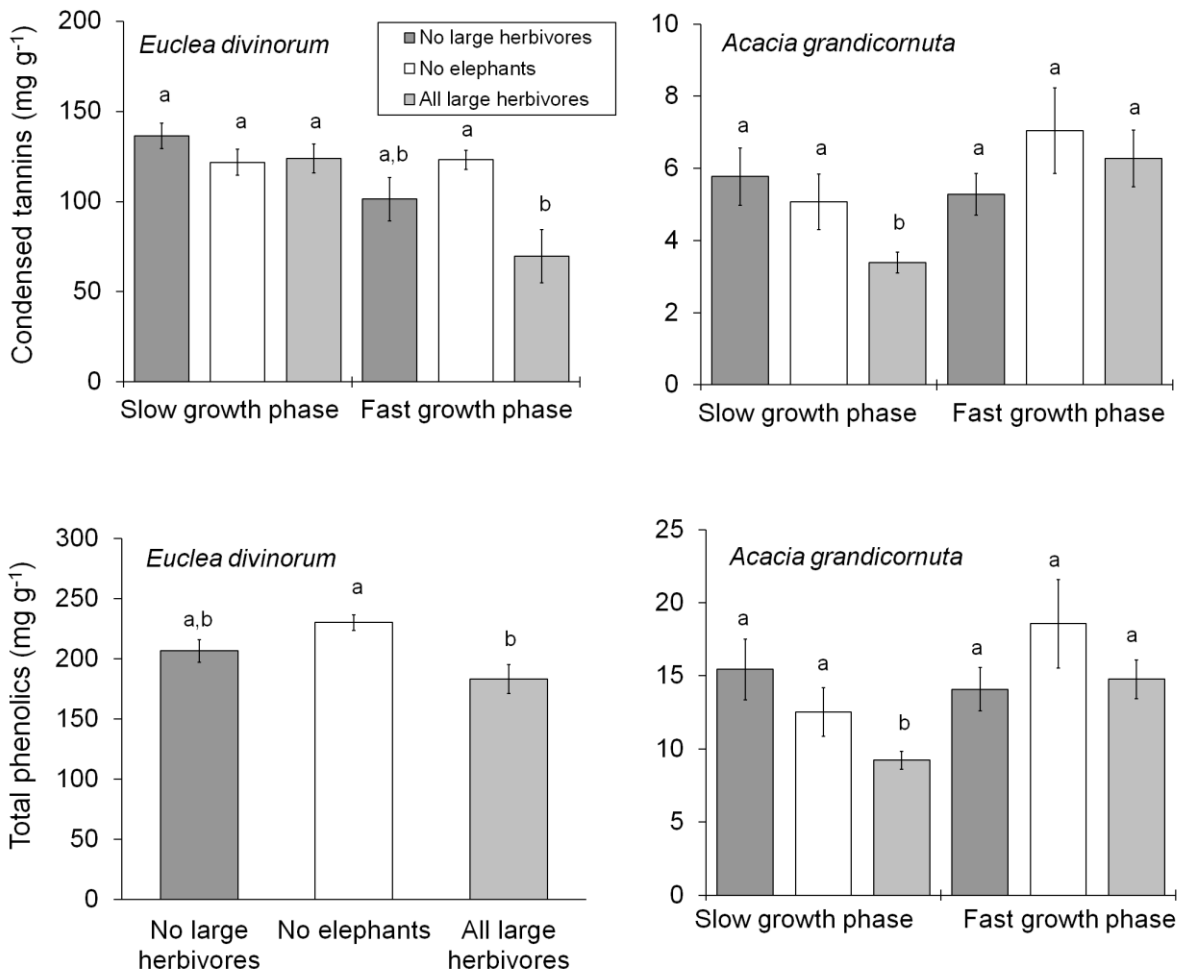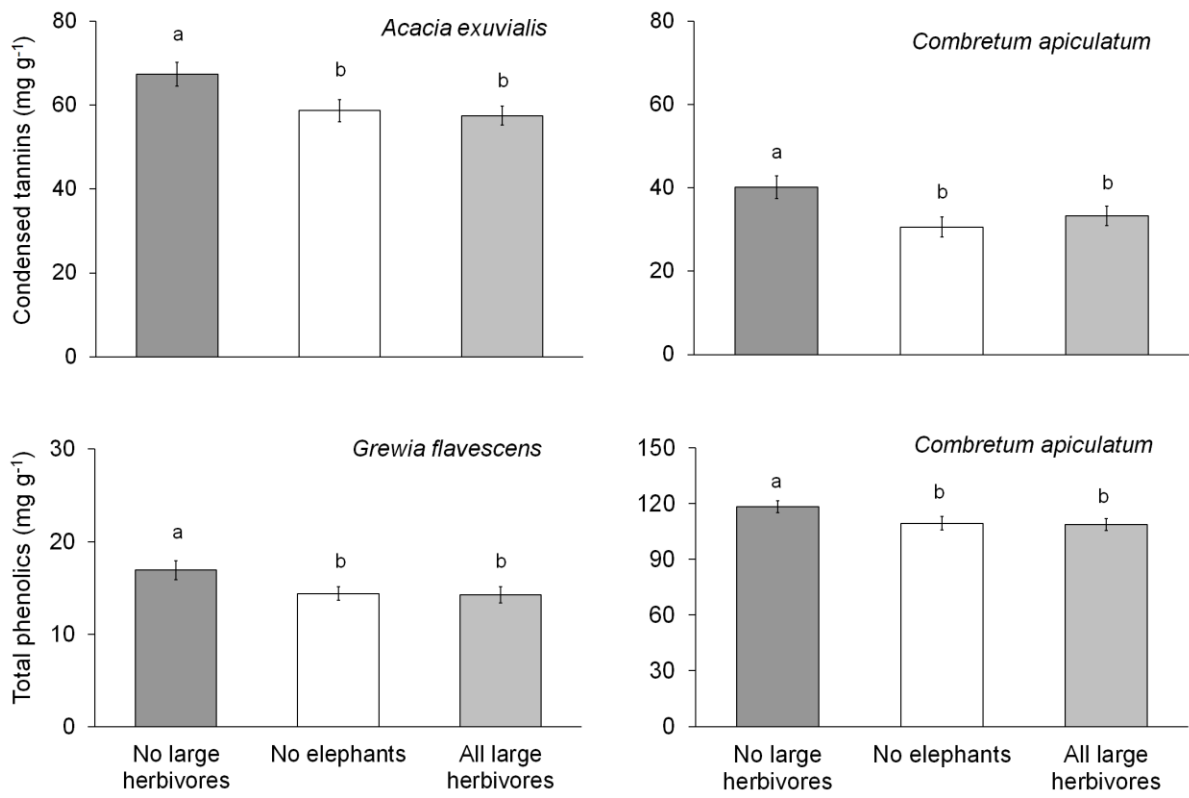**Fig. 2**

Fig. 3