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1 **Does large herbivore removal affect secondary metabolites, nutrients**
2 **and shoot length in woody species in semi-arid savannas?**

3

4 Peter F. Scogings^{a*}, Joakim Hjältén^b, Christina Skarpe^c

5 *^aDepartment of Agriculture, University of Zululand, Private Bag X1001,*

6 *KwaDlangezwa 3886, South Africa*

7 *^bDepartment of Wildlife, Fish, and Environmental Studies, Swedish University of*

8 *Agricultural Sciences, Umeå, Sweden*

9 *^cDepartment of Forestry and Wildlife Management, Hedmark University College,*

10 *Koppang, Norway*

11

12 *Corresponding author. Tel.: +27 35 9026063; fax: +27 35 9026056.

13 *E-mail address:* pscoging@pan.uzulu.ac.za (P. F. Scogings)

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26 **Abstract**

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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51 **1. Introduction**

52

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

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

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

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;

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 (Hrubar 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.

113

114

115 **2. Material and methods**

116

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/km² (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.

149

150 2.2. Sampling

151

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

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 N₂-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.*

300 *apiculatum* and *G. flavescens* are produced on long-shoots with one or two leaves per
301 node (Schmidt et al., 2007). Species with the latter growth pattern cannot produce
302 new photosynthetic tissues without first producing new somatic tissues, which
303 requires plenty of water and N (Ganqa and Scogings, 2007). We postulate that
304 required resources were not sufficient at the time of sampling to meet the
305 requirements of long-shoot production, leading to the lack of exclusion effect on shoot
306 length in *C. apiculatum* and *G. flavescens*. Nevertheless, our evidence altogether
307 indicates that shoot growth rate increases under browsing pressure, which supports
308 other studies (Fornara and du Toit, 2007; Hrabar et al., 2009).

309 The decrease in both shoot length and [TP] in *D. cinerea* following exclusion of
310 large herbivores (the latter contradicting our predictions) suggests that herbivory does
311 not necessarily result in C limitation in deciduous trees, which supports studies among
312 boreal species (Nykanen and Koricheva, 2004; Palacio et al., 2008). However,
313 responses to browsing may be modified by the frequency of browsing, nutrient
314 availability, the timing of damage and the plant tissue sampled (Hjältén et al., 1993,
315 1994; Lindroth et al., 2007). Plants accumulate C under nutrient stress (Herms and
316 Mattson, 1992), which could result in increased levels of CBSMs in browsed plants
317 (Rooke and Bergstrom, 2007). Alternatively, browsed plants may accumulate C from
318 compensatory photosynthesis and allocate some of it to increased CBSMs (Medhurst
319 et al., 2006; Olesen et al., 2008). If sufficient leaves remain after browsing,
320 photosynthesis contributes more than storage to the allocation of C to growth or
321 defence (*ibid.*). However, the relative contributions of compensatory photosynthesis
322 and storage to the increase in both [TP] and shoot growth in *D. cinerea* are unclear.
323 *Dichrostachys cinerea* is a fast-growing, aggressive invader that readily produces root
324 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.

347

348

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350

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360

361

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363

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497

498 **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

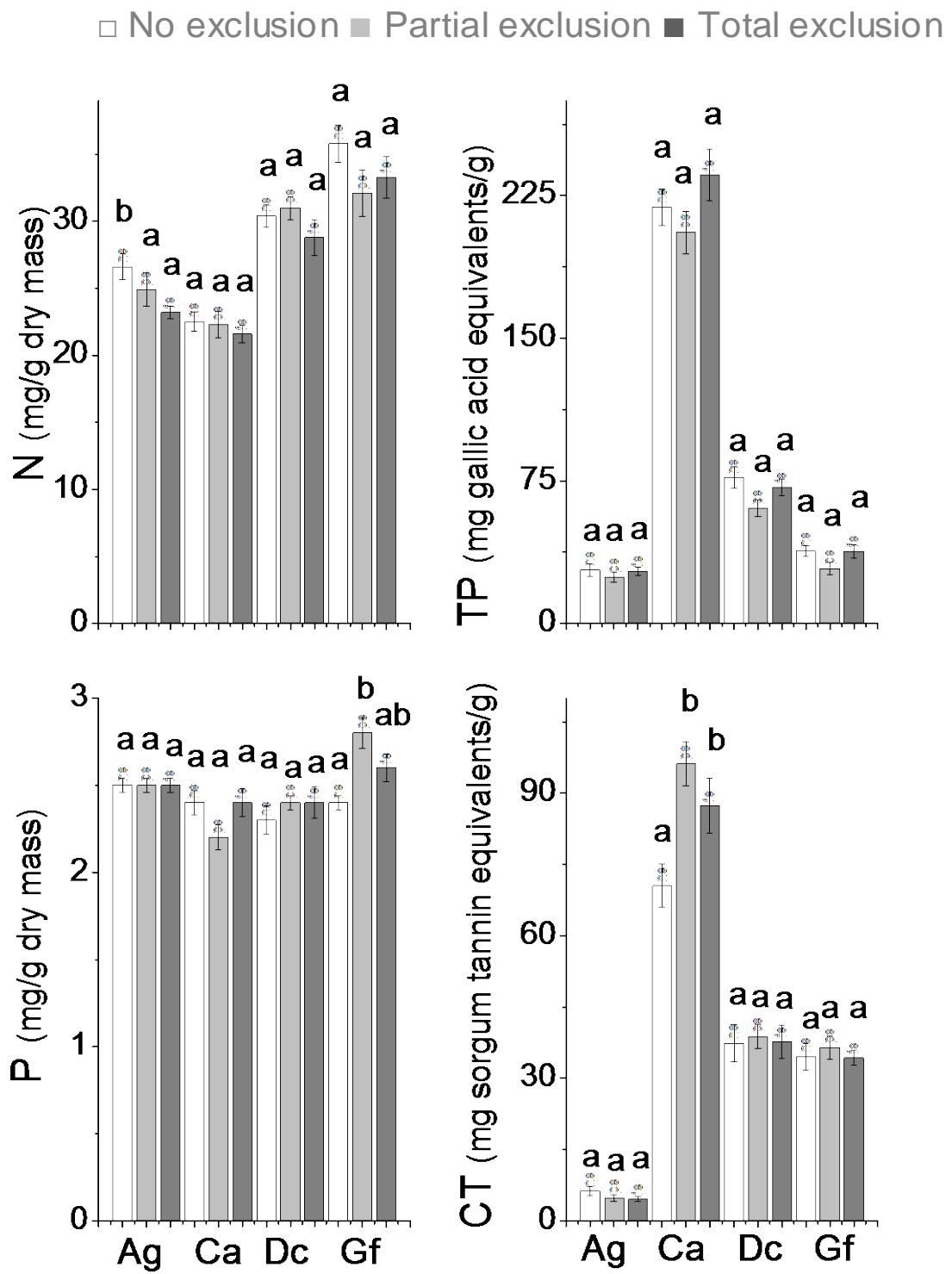


Figure 2

