Influence of soil, tree cover and large herbivores on field layer vegetation along a savanna landscape gradient in northern Botswana

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21   **Abstract**

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23   The response of the field layer vegetation to co-varying resource availability (soil nutrients,

24   light) and resource loss (herbivory pressure) was investigated along a landscape gradient

25   highly influenced by elephants and smaller ungulates at the Chobe River front in Botswana.

26   TWINSPAN classification was used to identify plant communities. Detrended

27   Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were used

28   to explore the vegetation-environment relationships. Four plant communities were described:

29   *Panicum maximum* woodland, *Tribulus terrestris* woodland/shrubland, *Chloris virgata*

30   shrubland and *Cynodon dactylon* floodplain. Plant height, species richness and diversity

31   decreased with increasing resource availability and resource loss. The species composition

32   was mainly explained by differences in soil resources, followed by variables related to light

33   availability (woody cover) and herbivory, and by interactions between these variables. The

34   vegetation structure and species richness, on the other hand, followed the general theories of

35   vegetation responses to herbivory more closely than resource related theories. The results

36   suggest a strong interaction between resource availability and herbivory in their influence on

37   the composition, species richness and structure of the plant communities.

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39   **Keywords**: Browsing; Grazing; Elephant; Plant community; Vascular plant; Soil property

40

1. Introduction

The species composition and diversity of vascular plant communities have been described as the outcome of resource availability, e.g. nutrients, water and light; and of the pattern of loss of resources or biomass, e. g., due to herbivory causing modification of species in evolutionary time and of community composition in ecological time (Grime et al., 1997; Pickett and White, 1985; Huntly, 1991). Resource availability is a determinant of primary productivity, which in turn has been suggested as a main determinant of species richness and abundance within many taxonomic groups, including plants themselves (Turner et al., 1987). Depending on spatial scale, habitat and taxonomic affiliation, species richness may be positively, negatively or unimodally related to primary production/resource availability (Turner et al., 1987; Waide et al., 1999). In plants a positive relationship may be expected for areas with low primary productivity, where increased plant production increases heterogeneity of resource availability, offering habitats for an increasing number of differently adapted species (Waide et al., 1999). At higher primary productivity, competition increases and species richness and diversity decreases due to competitive exclusion (Rosenzweig, 1971).

In savannas selective grazing/browsing and trampling by large herbivores are important agents in shaping plant communities by reducing height and biomass accumulation in the vegetation, and by differential impact on plant species (Walker and NoyMeir, 1982; Augustine and McNaughton, 1998). Loss of plant biomass, e.g. through herbivory, affects the competitive hierarchy of plants (McIntyre et al., 2003). While low frequency of tissue loss may lead to competitive dominance of a few species, and very high frequency may lead to exclusion of all but a few species, it has been hypothesised that an intermediate level of loss of biomass promotes species richness and diversity in communities (Connell, 1978).

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65   Differences in plant strategies in relation to resource availability and resource loss lead

66   to different compositions of plant communities along such gradients. Grime (1997) described

67   plants as adapted along three primary axes of specialisation, constant shortage of resources

68   (stress tolerators), high competition in resource rich environments (competitors), and high

69   frequency of loss of biomass (ruderals). The combination of these factors varies continuously

70   in the space between the three axes, and so do the combinations of adaptive mechanisms in

71   plant species. As adaptations in plants are largely species specific, the species composition of

72   plant communities is predicted to vary along the same axes. As environmental conditions in

73   real space vary over time, the species composition of plant communities also reflects long-

74   and short term temporal variation in environmental conditions.

75   In dry savannas large-scale vegetation patterns may be determined primarily by

76   rainfall, whereas landscape-scale variation in vegetation has been found to relate primarily to

77   soil resources, which in a landscape scale define the difference between dystrophic, low-

78   productive savanna and eutrophic high-productive savanna. This, in turn, has profound effects

79   on herbaceous plant communities directly via soil resource availability and indirectly by

80   influencing woody growth and patterns and intensity of herbivory (Scholes and Walker

81   1993).

82   We studied field layer vegetation along gradients in resource availability (soil

83   nutrients and light availability) and loss of biomass (herbivory) in a semi-arid savanna, with

84   the purpose of assessing the relative importance of these factors and their interactions in

85   influencing plant species community composition, richness and diversity. We expected soil

86   resources to be the main determinant of plant community composition, and light availability

87   and herbivory to have additional and interactive influence on community characteristics.

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89   **2. Study area**

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91   The study area is located in the northern part of Chobe National Park, Botswana. It

92 encompasses a ca 50 km x 10 km strip from Kasane in the east to Ngoma Bridge in the west,

93 limited in the north by Chobe River and in the south by the Kasane – Ngoma tarmac road

94 (Fig. 1). The area belongs to the Zudano – Zambezian biogeographical region (Werger 1978).

95 Based on aerial photographs from 1998 and field observations of the woody vegetation, the

96 area has, for other purposes, been classified into five different land cover types: 1) Floodplain,

97 2) *Capparis tomentosa* shrubland, 3) *Combretum* shrubland, 4) Mixed woodland and 5)

98 *Baikiaea plurijuga* woodland (Skarpe et al., 2004). In general, the sequence of the land cover

99 types follows the distance from the river along changing soil types, and the woody cover

100 increases with increasing distance from the river.

101   The climate is classified by Werger (1978) as BSh (arid, stepp climate, dry-hot in

102 Köppens classification) with an annual rainfall of about 640 mm occurring mainly in summer

103 between November and April (Botswana Meteorological Service Department, unpubl. data).

104 October is the hottest month with a mean daily maximum temperature of 39°C and a mean

105 daily minimum temperature of 14°C. July is the coldest month with a mean maximum

106 temperature of 30°C and a mean minimum temperature 4°C.

107   The floodplain consists mainly of alluvial deposits from the Chobe River. Calcic

108 gleysol and fluvisol are found close to the river and calcic luvisol covers the higher elevated

109 parts of the floodplain, adjacent riverbanks and a narrow strip (0-3 km) behind the riverbanks

110 (FAO, 1990). Further to the south the soils consist of deep, sandy and porous ferralic arenosol

111 (Kalahari sand) generated from aeolian deposits of sand and silt from the Kalahari sand beds.

112 Soil fertility generally decreases with the distance from the river (this study).

113   The study area is heavily grazed and browsed by increasing populations of elephants

114 (*Loxodonta africana*), buffalo (*Syncerus caffer*) and other large herbivores (Vandewalle,

115 2003). Particularly in the dry season animals aggregate close to the Chobe River, which is the

116 only permanent source of surface water. As a result of the increasing populations of

117 herbivores, the cover of both woody and herbaceous vegetation close to the river have

118 undergone profound changes during the last four decades as described in recent studies by

119 Mosugelo et al. (2002), Skarpe et al. (2004) and Moe et al. (2009) and by comparisons with

120 older records (Simpson 1975; Barnes 2001).

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122 **3. Material and methods**

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124 *3.1 Selection of sites and recording of vegetation data*

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126   Five transects were established along existing firebreaks, which are aligned in a north-

127 south direction, perpendicular to the river, running through the different land cover types (Fig.

128 1). Three permanent sampling sites, each 20 m x 20 m, were systematically placed in each

129 type along each transect at 50 m perpendicular distance from the firebreaks. Sites within each

130 land cover type along each transect were equidistant from each other. Due to differences in

131 the distribution of types along the transects, 12 sites were established on Floodplain, 13 in

132 *Capparis* shrubland and 15 in each of the *Combretum* shrubland, Mixed woodland and the

133 *Baikiaea* woodland, making a total of 70 sites. The lowest part of the floodplain was under

134 water at the time of study, and was not included.

135   The field layer vegetation, defined as all herbaceous plants and woody plants less than

136 50 cm in height, was analysed in five randomly distributed 1 m x 1 m sample plots in each

137 site. In total 350 sample plots were analysed. The cover of each species and the total cover of

138 the field layer vegetation were estimated on a percentage cover scale of 1-100%. The mean

139 height (cm) of the field layer was also recorded. All plots were analysed once in the mid-wet

140 season between January and March, from 1999 to 2002.

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143 *3.2 Sampling and recording of environmental variables*

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145 Explanatory variables (Økland et al., 2001) were sampled or recorded in relation to the

146 plots. The percentage canopy cover of trees (woody plants > 3 m tall) and shrubs (woody

147 plants between 0.5 and 3 m tall) over-layering the plots was estimated and used as an inverse

148 indirect variable for light reaching the field layer or the ground. Soil was classified in types by

149 eye as either alluvial soil (may consist of fluvisol and luvisol), Kalahari sand (arenosol), or a

150 mixture of alluvial soil and Kalahari sand. Soil samples for chemical analyses were collected

151 in the mid-wet season over the same four year period as the vegetation data (1999-2002).

152 Three soil cores, randomly distributed, were taken at 0-15 cm depth from each site. The soil

153 samples were air-dried in the field.

154 Grazing and browsing were subjectively quantified as the proportion of the total

155 biomass of each species that had been eaten (%), and summed for all species grazed/browsed

156 within the plot. Occurrence of faeces and signs of trampling by animals were recorded within

157 each plot as either present or absent as an indirect measure of herbivore presence. In addition

158 aspect (compass degrees), slope (degrees), topography (concave, flat or convex, subjectively

159 scaled from –3 to + 3) and percentage cover of detached litter and of bare soil were recorded

160 from each sample plot.

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163 *3.3 Soil chemical analyses*

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165   The soil samples were analysed for pH in $CaCl_2$ solution. Exchangeable calcium (Ca),

166   magnesium (Mg), sodium (Na) and potassium (K) and cation exchange capacity (CEC) were

167   analysed by 1 M ammonium acetate extraction at pH 7, extractable phosphorus (P) by Bray

168   method (Bray and Kurtz, 1945) and organic carbon (C) by wet oxidation (Walkey and Black,

169   1965; Nelson and Sommers, 1982). All chemical analyses were carried out at the Sebele

170   Agricultural Research Soil and Plant Analysis Research Support (SPARS) Laboratory in

171   Botswana.

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174   *3.4 Nomenclature, species and taxon concepts*

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176   Nomenclature for woody species follows Coates-Palgrave (2002) and for forbs and

177   graminoids Barnes et al. (1994), except the genus *Chamaecrista* Moench. and the species

178   *Eclipta alba* (L) Hassk. The species *Ambrosia artemisifolia* L, *Ipomoea pes-tigridis* L, *Leucas*

179   *martinicensis* (Jacq.) R. Br., *Sporobolus africanus* (Poir.) Robyns & Tournay and *Thunbergia*

180   *reticulata* A. Rich. were not listed in Barnes et al. (1994).

181   Species that could not be identified were either classified by their genus name or

182   growth form (shrub, grass or forb). No distinction was made between the grasses *Digitaria*

183   *milanjiana* and *Digitaria eriantha* , between the forbs *Commelina benghalensis* and

184   *Commelina livingstonia*, *Sida alba* and *Sida cordifolia* and between *Harpagophytum*

185   *procumbens* and *Harpagophytum zeyheri*. Thus, these "taxa" may consist of more than one

186   species.

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3.5 Data analyses

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191   The vegetation data were classified into plant community groups with two-way

192 indicator species analysis (TWINSPAN version 2.1b, Hill (1979a), modified by ter Braak and

193 H.J.B. Birks in 1983). TWINSPAN was chosen for the classification as we expected a strong

194 dichotomy in the data caused by soil differences, and because this method uses much thesame

195 algorithm as the ordination described below. Species with an uncertain identification were

196 given a non-negative weight of 0.01. The final TWINSPAN plant community groups were

197 subjectively chosen on the basis of their eigenvalues and evaluation of the species

198 composition between the groups. Detrended correspondence analysis (DCA) (Hill, 1979b;

199 Hill and Gauch, 1980) was used to explore the major patterns in species composition. The

200 relationship between the variation in species composition and the observed environmental

201 variables was explored with DCA using passive environmental variables and by canonical

202 correspondence analysis (CCA) (ter Braak, 1986; 1987).

203   The chemical variables of the three soil cores within a site were averaged and used for

204 all the five sample plots within the same site. All other environmental variables were recorded

205 within each vegetation plot. Only variables significantly related to the variation in species

206 composition ($p < 0.01$), either in a CCA of each environmental variable alone (marginal

207 effects) or in forward selection of environmental variables (conditional effects), as assessed

208 by Monte Carlo permutation tests (cf. ter Braak and Smilauer, 2002) were used in the

209 analyses. Slope, topography, aspect and the mixed soil type were excluded due to their low

210 explanatory power.

211   Variance partitioning, performed by partial CCA (Borcard et al., 1992; Økland and

212 Eilertsen, 1994; Aarrestad, 2002), was used to explain the variation in the species data in

213 relation to three different sets of explanatory variables related to resource availability and

214 herbivory:

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216   A) Soil resources (alluvial soil, Kalahari sand, pH, organic C, extractable P, exchangeable

217   Ca, Mg, Na, K and CEC)

218   B) Light availability (tree cover, shrub cover)

219   C) Herbivore impact (herbivory, faeces, trampling)

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221   All multivariate statistical analyses were performed with CANOCO 4.5 (ter Braak and

222 Smilauer, 2002). Default options were selected in DCA and CCA except that non-negative

223 weight was given to the same species or taxa as in the TWINSPAN classification, that rare

224 species (according to the definition in the CANOCO program) were down-weighted, and that

225 the percentage cover data of the species were square root transformed, due to the large

226 variation in percentage cover (1-100%).

227   Species richness of plant communities was calculated as the total number of species

228 occurring within the plots grouped to one community, and as the average number of species

229 per plot within the same community. Species diversity was calculated using Shannon diversity

230 index on average species abundance values from all plots within each plant community. The

231 species richness and diversity values are probably biased due to different number of plots

232 within each community. However, due to the large number of plots we find the method useful

233 for interpretation of diversity at the vegetation type level.

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236 **4. Results**

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238   *4.1 Classification and ordination of plant communities*

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240   Four plant communities were selected from the TWINSPAN classification and named

241   after the most important indicator species and land cover types as 1) *Panicum maximum*

242   woodland, 2) *Tribulus terrestris* wood- and shrubland, 3) *Chloris virgata* shrubland and 4)

243   *Cynodon dactylon* floodplain (Table 1; description below). The separation in each division

244   was strong as shown by high eigenvalues between 0.805 and 0.523. The DCA ordination

245   showed a strong first axis with an eigenvalue of 0.864 and a length of 7.2 standard deviations

246   (Fig. 2). The total variation in the species data was high as reflected by a total inertia of 10.4,

247   and the percentage variance in species composition explained by the first four axes was

248   18.8%.

249   The TWINSPAN derived plant communities were fairly well separated along the first

250   DCA axis (Fig. 2). However, there was an overlap of sample plots between woodland and

251   shrubland communities, indicating that these communities had several species in common.

252   The *Panicum* woodland community showed the largest variation in species composition

253   reflected by the relatively wide distribution along DCA axis 2.

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256   *4.2 Relationships between species composition and environmental variables*

257   The fitting of environmental variables in the DCA ordination showed that the strong first axis

258   is primarily related to soil nutrients and the contrast between alluvial soil and the Kalahari

259   sand, while the second axis is mainly related to woody cover (Fig. 2).

260   The CCA ordination showed a similar sequence of samples along the first axis as the

261   DCA, but with more variation along the second axis (Fig. 3). The eigenvalue of the strong

262   first axis was 0.770 and of the second axis 0.401. The first canonical axis explained 36.3%,

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263   the second 55.2%, and the first four axes 72.8% of the variation in species composition

264   explained by the recorded explanatory variables.

265   The most important variables were related to resource availability variables, such as

266   soil nutrients, soil type and woody cover (Table 2). Herbivory related variables, trampling,

267   faeces and herbivory were less important This pattern was also verified by the method of

268   variance partitioning (Table 3), where approximately 20% of the variation in the species

269   composition could be explained by the selected environmental variables. Soil variables had

270   the highest explanatory power followed by light, and herbivory impact and co-variation

271   (interaction) between environmental variables were important for some of the variation in

272   species composition (Table 3).

273   The first axis in the CCA biplot ordination diagram (Fig. 3) represented a gradient in

274   soil chemical elements related to the occurrence of alluvial soil and Kalahari sand, while the

275   main variation in environmental variables along the second axis was related to the amount of

276   bare soil, litter cover and soil pH. The direct herbivory variable was positively correlated with

277   the second axis, while the indirect herbivory variables faeces and trampling were correlated

278   with the first axis and both axes, respectively (Fig. 3). The third axis (not visualised here)

279   represented a gradient in woody cover.

280   Sample plots on alluvial soil representing *Cynodon* floodplain and *Chloris* shrubland

281   were along the first CCA axis well separated from most of the sample plots on Kalahari sand

282   represented by *Tribulus* wood- and shrubland and *Panicum* woodland (Fig. 3). Plots

283   representing the *Cynodon* floodplain were along this axis well separated especially from the

284   *Panicum* woodland plots and the *Tribulus* wood- and shrubland plots. The *Chloris* shrubland

285   plots showed an intermediate distribution on the same axis, and they were fairly well

286   separated from the other communities also on axis two. Some sample plots from the wood-

287   and shrubland communities overlapped in characteristics and thus reflect similar

288   environmental condition.

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291   *4.3 Plant community characteristics*

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293   The *Panicum maximum* woodland was highly associated with the Kalahari sand and had low

294   values of exchangeable cations and low values of herbivory related variables (Table 4). It was

295   characterized by a tall grass dominated field layer. It was a species-rich community and had

296   the highest species diversity   of all the described plant communities (Table 1). A large

297   number of shrubs, forbs, grasses and sedges had their optimum distribution in this community

298   (Table 1), and several species were restricted to this community. The dominating grasses were

299   *Dactyloctenium giganteum*, *Digitaria eriantha/milanjiana*. (Table 1).

300   The *Tribulus terrestris* wood- and shrubland was associated mainly with the Kalahari

301   sand. However, values of exchangeable cations and pH and signs of herbivory were higher

302   than in the *Panicum* woodland, and tree- and shrub cover were lower (Table 4). The

303   community was characterized by a grass- and forb dominated field layer of a lower stature

304   than in the *Panicum* woodland (Table 1) . It was a relatively species rich community and the

305   species diversity was only slightly lower than in the *Panicum* woodland (Table 1). The field

306   layer was dominated by the forb *Tribulus terrestris* and the grass *Urochloa* cf. *trichopus*.

307   None of the recorded species was strictly associated with this community. The community

308   had several species in common with the *Panicum* woodland (Table 1).

309   The *Chloris virgata* shrubland community occurred on alluvial soils close to the

310   floodplain but raised several meters above it. The soil had higher values of exchangeable

311   cations and pH than the communities on the Kalahari sand, and the mean P content and signs

312 of herbivory were the highest of all communities (Table 4). The *Chloris virgata* shrubland

313 was a relatively species-rich community, but over all species diversity was somewhat lower

314 than in the woodland communities (Table 1).

315   The *Cynodon dactylon* floodplain community was distributed on alluvial soil and

316 inundated by the Chobe River once each year, and, thus, hydrologically very different from

317 the shrub- and woodland communities. There was no tree- or shrub layer. The soil had the

318 highest values of exchangeable cations and CEC and the lowest pH of all the communities

319 (Table 4). The field layer was characterized by dense carpets of *Cynodon dactylon*.,Species

320 richness was low and the species diversity was lowest of all communities. The community

321 was dominated by the grass *Cynodon dactylon* and the forb *Heliotropium ovalifolium*. Several

322 species, primarily grasses, were more or less restricted to this community (Table 1).

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325 **5. Discussion**

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327 *5.1 Effects of resource availability and herbivory on plant community composition*

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329   As expected for savanna vegetation (Scholes and Walker 1993), the most important

330 explanatory variables for herbaceous plant community composition were related to resource

331 availability, primarily soil resources, with herbivory related variables being the least

332 important. Similar results have been obtained for other arid and semi-arid regions (Milchunas

333 and Lauenroth 1993) . Nine soil variables had higher explanatory power than any variables

334 related to light availability (woody cover) or herbivory impact (Table 2). The four plant

335 communities were sequentially arranged along the first two DCA and CCA axes (Fig. 2 and

336 3) primarily representing soil fertility, demonstrating an increase in soil fertility along the

337   landscape gradient from the *Panicum* woodland to the *Cynodon* floodplain. The differences in

338   soil fertility were mainly related to the different soil types, but particularly within the alluvial

339   soils there is a great difference between soil variables in the *Chloris virgata* shrubland and the

340   *Cynodon dactylon* floodplain. The Kalahari sand and the more clayey alluvial soils differ not

341   only in chemistry but also in texture and structure. This implies differences in soil moisture

342   conditions, which might be more favourable for plant growth, particularly for deep rooted

343   perennial forbs, on the Kalahari sand than on the fine-textured alluvial soils (Walker and

344   NoyMeir, 1982). Soil moisture was, however, not recorded in the study. The *Panicum*

345   woodlands and the *Tribulus terrestris* wood-and shrubland were almost not separated along

346   the negative side of the first CCA axis (Fig. 3). The low nutrient status of these communities

347   is due to the coarse and nutrient deficient Kalahari sand and to the nutrient poor and slowly

348   decomposed leaf litter from the broad-leafed phenolic-rich trees, making up most of the plant

349   biomass (Campbell et al., 1994; Scholes and Walker, 1993). Elephants probably play an

350   important indirect role in nutrient cycling in the woodlands, by   turning large amounts of

351   nutrient poor biomass into easily decomposable faeces and urine (Botkin et al., 1981), and

352   making it possible for relatively nutrient demanding species such as *Panicum maximum* and

353   *Digitaria* spp. to grow there. The low concentration of organic carbon in the woodland soil

354   might be caused by slow decomposition rates of litter, nutrient seepage to the bottom floor of

355   Kalahari sands, transportation of carbon in the form of foliage to the riverfront, and by

356   historically important fires (Masunga, 2008), in which carbon was lost to the atmosphere in

357   the form of carbon-dioxide. Älvgren (2008) has shown a considerable net import of nutrients

358   in dung and urine by elephants to the floodplains. In the *Tribulus* shrub- and woodland more

359   fast-growing woody species with easier decomposable litter are more common (Skarpe et al.,

360   2004) and may be a reason for the slightly higher exchangeable cation concentrations. Many

361   of the soil variables were distinctly higher on the floodplain than in any of the other

362 communities (Table 4). Some of this may be caused by water-deposited minerals from the

363 annual flooding, reflected by the relatively high concentration of Na and P (Mubyana et al.,

364 2002). The high values of exchangeable elements may also be related to the rapid recycling

365 from faeces and urine from grazing and drinking animals (Georgiadis and McNaughton, 1990;

366 Mathisen, 2005). Soil pH was quite low on the floodplain, probably caused by humic acids

367 produced during mineralization of the humus in the upper soil layer (Schroeder, 1984). This is

368 probably the reason why pH in this study is not positively correlated to calcium content, as

369 shown in most studies of relationships between soil and vegetation (e.g. Aarrestad, 2002).

370   Light availability, as the inverse of tree- and shrub cover (Table 4), was lowest in the

371 woodland communities on the Kalahari sand and highest on the fully open flood plain, but

372 seemed to have low explanatory power for the species composition (Table 2 and 3). This

373 variable should be interpreted with care, as we did not actually measure light, and woody

374 cover has many other effects beside the shade, for example on soil and air humidity and the

375 distribution of input of animal faeces and urine, as animals tend to rest in the shade of trees.

376   Direct and indirect indications of herbivory had the lowest explanatory power for

377 species composition (Table 3), as would be expected in a region with long history of grazing

378 and browsing. The indirect measures of herbivory or of time spent by animals in the sites,

379 herbivore faeces, and to some extent trampling, were positively related to CCA axis 1 (Fig. 3).

380 The more direct variable, signs of herbivory in the plots, was, however, better related to CCA

381 axis 2 and the *Chloris* shrubland. It is likely that signs of herbivory were underestimated in

382 the low, mat forming *Cynodon dactylon*, which compensates fast for lost tissue (Mathisen,

383 2005) and where herbivory, unless whole tufts are pulled out, will be little visible. The

384 herbivory impact probably affects the field layer height, which decreases significantly from

385 the *Panicum* woodland to the *Cynodon* floodplain (t-test between all communities p < 0.01),

386 and the field layer cover, which had the lowest value on the heavily grazed *Chloris* shrubland.

387 Thus, together with the distinct pattern of variation in animal faeces and trampling, there is

388 evidence to conclude that the herbivore impact increases from the woodlands to the

389 floodplains and affects the distribution and structure of plant communities.

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392 *5.2 Diversity and species richness*

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394 The length of the first DCA axis, 7.2 standard deviation units (Fig. 2) represents a very

395 high compositional turnover of species, and indicates large between-community (beta)

396 diversity within the analysed landscape gradient (Gauch and Whittaker, 1972; Økland, 1990).

397 Species richness and diversity declined with increasing resource availability from the

398 *Panicum* woodland to the *Cynodon* floodplain instead of peaking at some intermediate level

399 of resource availability, as expected. The dystrophic Kalahari sand in the subhumid *Baikiaea*

400 *plurijuga* dominated woodland can hardly be described as intermediate in resources even on a

401 larger scale. A more likely reason for the decline in diversity may be interaction between

402 resource availability and herbivory. It is known (Skarpe et al., 2004) that the nutrient rich

403 floodplains were more diverse or rich in species in a period when large herbivores were not as

404 abundant as today, and possibly the low herbivory pressure in the *Panicum* woodlands is a

405 reason for their comparatively high species richness.

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408 **6. Concluding remarks**We found vegetation structure and the species composition of

409 plant communities to vary along the joint resource and herbivory gradient from the woodland

410 to the floodplain. General theories predict different responses by vegetation to variation in

411 plant resources and in herbivory. We expected the species composition of the field layer to

412   vary with soil nutrient status, and field layer height and cover   to increase with increasing

413   resource availability whereas species richness and diversity would be expected to peak at

414   some intermediate level of resource availability and herbivory frequency (Huntly, 1991;

415   Grime et al., 1997). Although soil resources had the highest explanatory power for the

416   variation in species composition, the variation in species richness and diversity of the plant

417   communities and the variation in vegetation structure followed the expectations from the

418   herbivory gradient more closely. Thus, our results suggest a strong interaction between

419   resource availability and herbivory in their influence on plant communities both in species

420   composition, species richness and vegetation structure.

421   Our results confirm the strong dichotomy in savanna vegetation depending on whether

422   plant growth is limited primarily by nutrient availability (dystrophic savannas), or by moisture

423   (eutrophic savannas) and that this pattern in a landscape scale mainly is related to soil

424   productivity (Scholes and Walker 1993), in our case the difference between the alluvial soils

425   and the Kalahari sand. However, we also show that selective herbivory interacts with resource

426   availability and influences for example species richness and vegetation structure.

427

428

436   DWNP staff in Kasane and in Gaborone for their help and assistance throughout the study

437   period.

438

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555

Tables

557 Table 1. TWINSPAN derived plant communities along the Chobe River of Chobe National

558 Park, Botswana. Species showing an optimal distribution within the communities. * are

559 preferential species in the TWINSPAN context. Indicator species (the most important

560 preferential species) are shown in bold face. Number of sample plots (N), total number of taxa

561 per community (Tot sp.), mean number of taxa per sample plot (Mean sp.), Shannon diversity

562 index (S-index), mean cover of field layer (F cover) in %, mean height of field layer (F

563 height) in cm, all shown per community

564

	Panicum maximum woodland	*Tribulus terrestris* wood- and shrubland	*Chloris virgata* shrubland	*Cynodon dactylon* floodplain
Shrubs				
	Baikiaea plurijuga	Combretum elaeagnoides	Capparis tomentosa	
	Baphia massaiensis*	Combretum mossambiscense	Fluegga virosa	
	Bauhinia petersiana*	Clerodendrum ternatum		
	Combretum apiculatum	Croton megalobotrys		
	Combretum celastroides	Dicrostachys cinerea		
	Combretum engleri			
	Combretum molle			
	Croton gratissimus			
	Diplorhynchus condylocarpon			
	Friesodelsia obovata*			
	Jasminium stenolobum			
	Markhammia obtusifolia			
Forbs				
	Commelina africana	Cleome hirta	Acanthospermum hispidum	Ambrosia artemisifolia*
	Commelina zambesica	Crotolaria ssp.	**Chamaecrista sp.***	Acalypha sp.
	Euphorbia crotonoides	Commelina benghalensis/ livingstonia*	Corchorus tridens*	Eclipta alba
	Harpagophytum procumbens/ zeyheri	Gisekia africana*	Duasperma quadrangulare	**Heliotrophium ovalifolium***
	Hemizygia bracteosa	Ipomoea pes-tigridis	**Indigofera spp.***	
	Hibiscus vitifolius	**Tribulus terrestris***	Sida alba/cordifolia	
	Ipomoea plebeia		Pupalia lappacea var. velutina	
	Jacquemontia tamnifolia			
	Micrococca mercurialis*			
	Mormodica kirkii			
	Oxygonum sinnatum			
	Rhynchosia totta var. totta			
	Spermacoce senensis			
	Triumfetta pentandra			
	Vigna cf. unguiculata*			
Grasses/ Sedges				
	Abildgaardia hispidula	Megaloprotachne albescens	Cynodon dactylon*	Brachiaria eruciformis
	Brachiaria nigropedata	Pogonarthria squarrosa	Cenchrus ciliaris	**Cynodon dactylon***
	Dactyloctenium giganteum	Schmidtia pappophoroides	**Chloris virgata***	Dactyloctenium aegypticum
	Panicum maximum*	**Urochloa cf. trichophus***	Eragrostis cilianensis	Digitaria maniculata
	Cyperus margaritaceus		**Eragrostis cylindriflora***	Echinochloa colona
	Mariscus dubius		Eragrostis sarmentosa	Panicum repens
	Mariscus laxiflorus		Tragus berteronianus	Sporobulus africanus
			Urochloa cf. trichophus*	Vetiveria nigritana*
N	139	102	49	60
Tot sp.	110	93	56	35
Mean sp.	8.4	7.4	7.8	4.0
S-index	3.2	3.0	2.8	1.3
F cover	31.7	32.4	24.9	43.6
F height	67.3	37.8	28.1	24.5

565

566

567 Table 2. The percentage variation (V) in the species data explained by the environmental

568 variables in a canonical correspondence analysis (CCA) of the field layer vegetation data, Chobe

569 National Park, Botswana, estimated with two different methods: V_1 marginal effects (one

570 variable at a time) and V_2 conditional effects (forward selection of variables).

571

Variable	λ_1	V_1	λ_2	V_2
CEC	0.67 **	6.47	0.67 **	31.59
C	0.60 **	5.79	0.05 **	2.36
Alluvial soil	0.59 **	5.70	0.32 **	15.08
Ca	0.57 **	5.50	0.08 **	3.77
Kalahari sand	0.51 **	4.92	0.06 **	2.83
Mg	0.45 **	4.34	0.07 **	3.30
Bare soil	0.32 **	3.09	0.13 **	6.13
pH	0.27 **	2.61	0.21 **	9.90
K	0.23 **	2.22	0.06 **	2.83
Litter cover	0.22 **	2.12	0.04 **	1.89
Na	0.19 **	1.83	0.08 **	3.77
Trampling	0.16 **	1.54	0.05 **	2.36
Shrub cover	0.13 **	1.26	0.08 **	3.77
Tree cover	0.12 **	1.16	0.09 **	4.24
Faeces	0.12 **	1.16	0.02 ns	0.94
P	0.12 **	1.16	0.04 *	1.89
Herbivory	0.12 **	1.16	0.07 **	3.30

572

573   λ_1 = eigenvalue of the first axis in a CCA with the one environmental variable.

574   V_1 = [λ_1/sum of all unconstrained eigenvalues in a CA, total inertia] x 100, (percentage variation in the species data explained by

575   the environmental variable alone, marginal effects).

576   λ_2 = eigenvalue of the first axis in a CCA with forward selection of the environmental variables.

577   V_2 = [λ_2/sum of all canonical eigenvalues in a CCA] x 100, (percentage variation in the species data explained by the variable in a

578   forward selection where the variation explained by the more important variables is removed, conditional effects).

579   ** = significant ($p \leq 0.01$), * = significant ($p \leq 0.05$) in Monte Carlo permutation tests (99 unrestricted permutations), ns = non

580   significant.

581

582

583 Table 3. Variation in species composition (in percentage) explained by sets of variables

584 related to soil characteristics (A), light availability (B) and herbivore impact (C) by methods

585 of variance partitioning. Chobe National Park Botswana.

586

Subset I	Subset II	V_1	V_2	V_3	V_t	V_u
A. Soil variables	(B + C)	13.8	2.4	3.1	19.3	81.7
B. Light availability	(A + C)	1.7	0.8	16.8	19.3	81.7
C. Herbivore impact	(A + B)	1.4	2.1	15.8	19.3	81.7

587

588 V_1: variation explained by subset I, when variation due to subset II is allowed for statistically (as covariables); V_2: variation

589 shared by subset I and II; V_3: variation explained by subset II, when variation due to subset I is allowed for statistically (as

590 covariables); V_t: Total variation explained by the variables (both subset I and subset II); V_u: the unexplained variation.

591

592

593 Table 4. Mean values and standard deviation (SD) of environmental variables found

594 statistically significant to the overall species variation within different TWINSPAN derived

595 plant communities. Plot variables are means of the 1x1 m sample plots classified to each plant

596 community, and soil chemical variables are means of soil samples taken within sites,

597 reflecting the same communities. n = number of samples. Chobe National Park, Botswana.

598

	Panicum woodland		*Tribulus* wood- and shrubland		*Chloris* shrubland		*Cynodon* floodplain	
Plot variables	*(n=139)*	*SD*	*(n=102)*	*SD*	*(n=49)*	*SD*	*(n=60)*	*SD*
Tree cover (%)	9.07	19.63	4.22	14.10	0.00	0.00	0.00	0.00
Shrub cover (%)	11.09	19.13	5.84	11.94	3.41	9.07	0.00	0.00
Litter cover (%)	23.37	23.21	9.08	9.23	7.41	5.02	28.83	29.82
Bare soil (%)	66.20	24.11	82.77	13.26	84.43	8.67	47.43	39.13
Herbivory (%)	2.86	6.56	6.30	11.50	17.33	17.01	4.13	10.83
Faeces	0.06	0.23	0.21	0.41	0.22	0.42	0.38	0.49
Trampling	0.50	0.50	0.65	0.48	0.90	0.31	0.88	0.32
Alluvial soil	0.01	0.12	0.14	0.35	0.90	0.31	1.00	0.00
Kalahari sand	0.97	0.17	0.75	0.44	0.08	0.28	0.00	0.00
Soil chemistry	*(n=82)*	*SD*	*(n=64)*	*SD*	*(n=32)*	*SD*	*(n=35)*	*SD*
pH	4.99	0.44	5.69	0.57	6.38	0.87	4.78	0.34
C (%)	0.42	0.12	0.58	0.35	0.68	0.18	4.69	3.18
P (mg/100g)	9.52	5.11	37.93	53.53	72.68	114.25	44.00	23.61
Ca (mg/100g)	21.44	13.55	60.21	61.21	161.92	149.24	424.95	270.37
Mg (mg/100g)	3.45	1.73	5.06	3.00	8.95	2.50	39.84	41.75
Na (mg/100g)	0.66	0.78	1.04	1.25	4.15	4.22	71.78	197.83
K (mg/100g)	6.47	10.62	9.97	7.78	24.44	26.22	32.60	44.81
CEC (meq/100g)	2.14	0.92	3.85	2.54	6.08	1.39	32.21	15.99

599

600   Herbivory (index) expressed in %. Faeces, Trampling, Alluvial soil and Kalahari sand as average of present/absent data. C
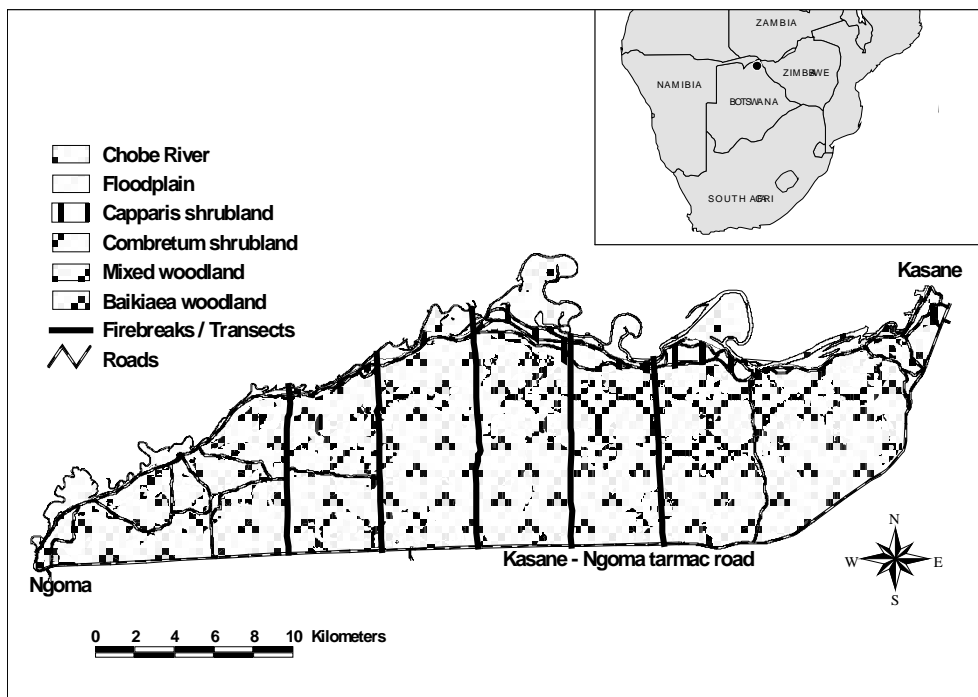
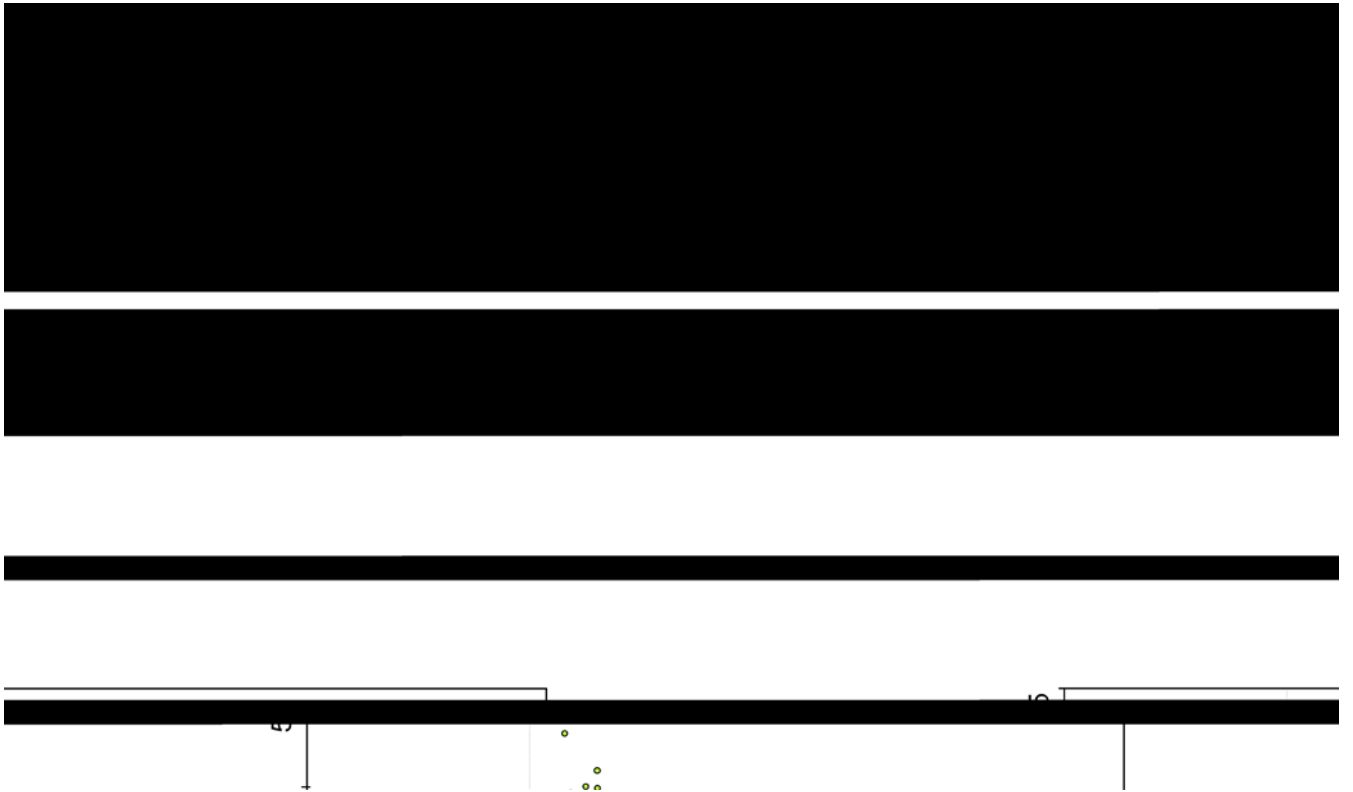601   (organic carbon) in weight %.

602

Figures

605

606

607 Fig. 1. The study area situated between Chobe River in the north and Kasane – Ngoma road

608 with land cover types and five sampling transects. Chobe National Park, Botswana. From
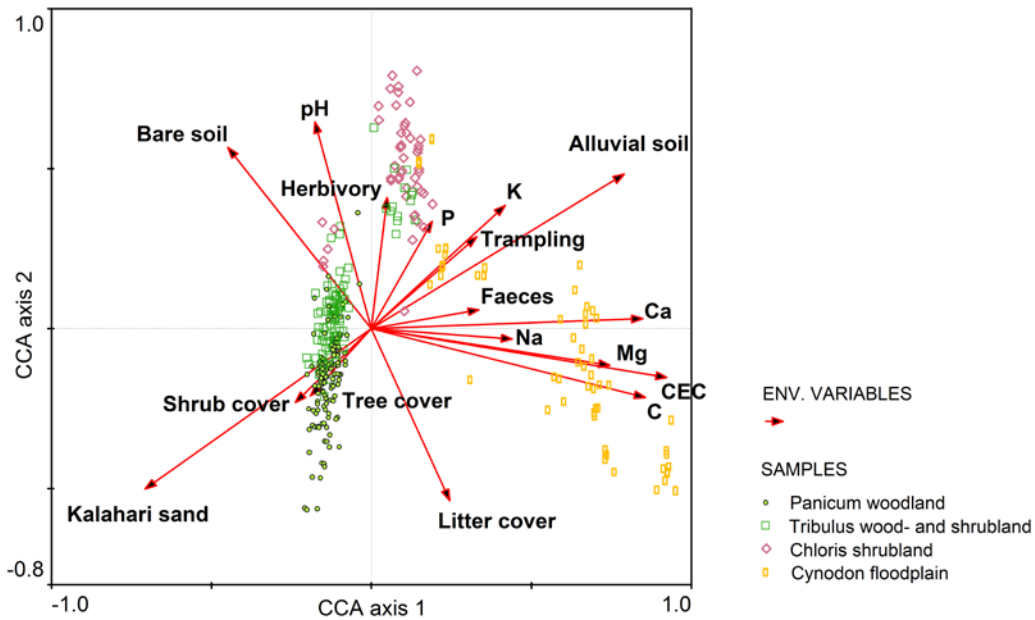
609 Skarpe et al. (2004).

610

612

Fig. 2. Detrended correspondence analysis (DCA) diagram, axis 1 and 2, of the field layer

vegetation data (sample plots) with their TWINSPAN derived plant community membership

and environmental variables fitted as arrows. Chobe National Park, Botswana.

616

617 Fig. 3. Canonical correspondence analysis (CCA) biplot diagram, axis 1 and 2, of

618 environmental variables and the field layer vegetation data (sample plots) with their

619 TWINSPAN derived plant community membership. Chobe National Park, Botswana.