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1 **Examination of multiple disturbances effects on herbaceous vegetation**

2 **communities in the Sudanian savanna-woodland of West Africa**

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19 **Abstract**

20 In West Africa policies for prescribed early fire, grazing and selective tree cutting in the

21 savanna-woodlands are rarely based on long-term experimental studies. The purpose of this

22 study was to provide scientific evidence based on field data from two case studies for an

23 informed discussion on the long-term response of herbaceous abundance both at the

24 community and individual species levels to fire, grazing, selective cutting and their

25 interactions. A long-term factorial experiment was established in two State forests reserve in

26 Burkina Faso, and mainly differing in their soil attributes. Community abundance data

27 recorded from line intercept sampling over 13 years, were analyzed using a multivariate

28 ordination technique known as Principal Response Curves (PRC).

29 The results indicate that disturbance regimes, independently or interactively, influenced

30 species abundance over time with inter-site specificity. The dynamics of these disturbance

31 regimes exhibited temporal variation which could be related, to some extent, to inter-annual

32 variation in annual rainfall. The PRC ordination accounted for 38% and 34% of the variation

33 within the data set for sites with deep and shallow soils, respectively. At the site with deep

34 soils, more than one PRC axis was needed to summarize the community response sufficiently,

35 suggesting that the species reacted in different ways to disturbances. The PRC method

36 approach to the analysis of disturbance dynamics allowed us to distil the complexity of the

37 community responses to those of individual species and to identify species that can serve as

38 indicators of certain disturbance regimes.

39

40 **Keywords:** Fire; herbivory; interactive disturbance; understory abundance; multivariate

41 ordination techniques; savanna ecosystem

1. Introduction

Savannas are often subjected to multiple anthropogenic disturbances, including grazing, browsing, fire and selective tree cutting (Breman and Kessler, 1995). These disturbance regimes are often regarded as sources of spatial patterning, diversity and community organisation in grasslands and woodlands (McNaughton, 1983; van Langevelde et al., 2003). Generally, the local species richness and the diversity of savanna ecosystems are maintained by dynamic interactions between local colonization from species pools at larger spatial scales and local extinction due to competitive exclusion. These are, in turn, influenced by disturbance (Gibson and Brown, 1991; Olff and Ritchie, 1998). In savanna woodlands, characterized by mixtures of woody and herbaceous life forms, understanding the effect of various types of disturbance on the herbaceous community is essential for designing multiple use management plans. This is because the herbs account for 75-90% (Frost and Robertson, 1987) of the total annual biomass in tropical savanna ecosystems and play a major ecological as well as socio- economic role (Le Mire Pecheux, 1995).

Current policies for sustainable management of savanna-woodlands in Burkina Faso focus on woody vegetation and entail prohibition of grazing, setting annual early fires and selective tree cutting of 50% of the basal area over a 20-year rotation (Bellefontaine et al., 2000). This approach is not based on scientific evidence. To generate scientific information to use in developing appropriate management strategies, long-term experimental plots were established in 1992 to examine the ecological effect of repeated burning, grazing and selective tree cutting on both the woody and herbaceous components of the Sudanian savanna woodland (Nygård et al., 2004; Savadogo et al., 2007; Sawadogo et al., 2002; Sawadogo et al., 2005; Zida et al., 2007). This ongoing experiment is generating large data sets, comprising information on temporal changes in the abundance of herbaceous vegetation in the control and

67   treatment plots. From these large datasets, however, only information about a limited number

68   of taxa (usually the most abundant ones) or overall means have, so far, been properly

69   analyzed with standard univariate statistical methods (Savadogo et al., 2007; Sawadogo et al.,

70   2005). Although such techniques are well documented and robust, in general they tend to

71   explain about half of the variation, as is usual for multivariate analysis in vegetation studies

72   (Grace, 1999). Previously, we applied repeated measures analysis, but it was not possible to

73   discern treatment effects at the level of individual species (Savadogo, 2007). In order to

74   obtain a complete picture of disturbance dynamics and their effect on the vegetation

75   community, an appropriate multivariate analysis technique that combines the interaction

76   between treatment and time effects, both at community and individual species levels is

77   needed.

78

79   In this study, the main research question was: how do the effects of disturbance regimes on

80   herbaceous vegetation abundance change over time? The research question could also be

81   phrased: what is the response, over time, of the herbaceous vegetation community to fire,

82   grazing and selective cutting disturbances? To answer these questions, the abundance of

83   herbaceous vegetation recorded over 13 years (1994-2006) was analyzed using a multivariate

84   ordination technique called Principal Response Curves (PRC). PRC analysis is an ordination

85   method based on partial redundancy analysis and developed specifically for analysis of

86   community response data from designed experiments sampled repeatedly over time (van den

87   Brink and ter Braak, 1998; 1999). Associated with each PRC is a set of species weights,

88   which reflect the influence of each species on the overall community response described by

89   the PRC scores over time.

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4

2. Materials and Methods

2.1 Site description

The experimental sites are located on flat areas in Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) State Forests (forêts classées), both at an altitude of 300 m a.s.l in Burkina Faso, West Africa. The Laba and Tiogo State Forests were delimited by the colonial French administration in 1936 and 1940 and cover 17 000 ha and 30 000 ha, respectively. Both forests are located along the only permanent river (Mouhoun, formerly known as Black Volta) in the country. Phyto-geographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (Fontes and Guinko, 1995). The vegetation type at both sites is a tree/bush savanna with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard as well as the perennial grasses *Andropogon gayanus* Kunth. (dominant in Tiogo) and *Andropogon ascinodis* C.B.Cl. (dominant in Laba). In the study area, these two perennial grasses are the most important species for fodder, local construction (roof-thatching and fences) and handicraft. The main forb species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC.) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Linn. Species in the families Mimosaceae and Combretaceae dominate the woody vegetation component at both sites. In terms of basal area, the main woody species are *Detarium microcarpum* Guill. & Perr., *Combretum nigricans* Lepr. ex Guill. & Perr., *Acacia macrostachya* Reichenb. ex Benth., *Entada africana* Guill. & Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpus* (DC.) Guill. & Perr. and *Vitellaria paradoxa* C.F. Gaertn. At Laba experimental site, at the beginning of the study period the mean basal area of woody species was 10.7 m^2 ha^{-1} at stump level (20 cm) and 6.3 m^2 ha^{-1} at breast height (130 cm) with a stand density of 582 individuals ha^{-1} for stems $\geq$10 cm GBH (girth at breast height). At Tiogo, the

116 equivalent figures were 10.9 m^2 ha^{-1} at stump level, 6.1 m^2 ha^{-1} at breast height and 542

117 individuals ha^{-1}.

118

119 The unimodal rainy season lasts for about six months, from May to October. The mean (± SE)

120 annual rainfall (Fig. 1) during the period (1994-2006) was 869 ± 39 mm for Laba and 848 ±

121 49 mm for Tiogo, and the number of rainy days per annum was 69 ± 5 and 66 ± 3 for Laba

122 and Tiogo, respectively. Mean daily minimum and maximum temperatures are 16°C and 32°C

123 in January (the coldest month) and 26°C and 40°C in April (the hottest month), yielding an

124 aridity index (Brown and Lugo, 1982) of 3.5 and 3.7 for Laba and Tiogo, respectively. Most

125 frequently encountered soils are Lixisols (Driessen et al., 2001), and the soil at Laba is

126 shallow (< 45 cm depth) silty-sand while it is mainly deep (>75 cm) silty-clay at Tiogo. These

127 soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998).

128

129 *2.2 Experimental design*

130 A factorial experiment was established in each of the two state forests to examine the effects

131 of grazing, early fire, selective cutting and their interaction on abundance of herbaceous

132 vegetation (Fig. 2). Each experimental site (18 ha) was divided into eight blocks (2.25 ha);

133 four of which were fenced to exclude livestock (hereafter refereed to as non-grazed plots) and

134 the other four were open for grazing (hereafter referred to as grazed plots). Each block was

135 further divided into four plots of 0.25 ha (50 x 50 m), separated from each other by 20 – 30 m

136 fire-breaks. To the four plots within each block, the following treatments were randomly

137 assigned: No cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire.

138 The selective cutting was done in December 1993 at Tiogo and a month later in January 1994

139 at Laba by removing 50% of the basal area at stump level. Prior to cutting, all species were

6

140   categorized according to their local uses as protected species, timber, poles and fuelwood, and

141   fuelwood and others (Hagberg et al., 1996; Sawadogo, 1996). Except protected species,

142   individuals of other categories were cut according to the following size criteria: > 30 cm butt

143   diameter for timber species, > 14 cm diameter at stump level for poles and fuelwood species

144   and > 8 cm diameter at stump level for fuelwood and others (Sawadogo et al., 2002). The

145   prescribed early fire was applied at the end of the rainy season (October – November) each

146   year beginning 1993 when the grass layer humidity was approximately 40%. The grazing

147   main plots at both study sites were open for grazing by livestock (a mixed herd of cattle,

148   sheep and goats) mainly but also wild animals. The livestock carrying capacity in Laba forest

149   was 1.0 tropical livestock unit ha^{-1} (T.L.U. ha^{-1}) and that of Tiogo was 1.4 T.L.U. ha^{-1}

150   (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity

151   (Sawadogo et al., 2005). The presence of the livestock in the two forests varied spatially and

152   temporally; grazing mainly occurs during the rainy season when grasses were green and

153   surrounding area cultivated.

154

155   *2.3 Data collection and analysis*

156   The abundance of herbaceous vegetation was assessed every year from 1994 to 2006 at the

157   end of the rainy season (September to October) when most of the species are flowering and

158   fruiting, which allows for easy species identification. The point-intercept sampling procedure

159   (Levy and Madden, 1933) was used to gather species-cover data. The presence of species was

160   recorded along a 20 m permanent line laid in each subplot at an interval of 20 cm, giving a

161   total of 100 sampling points. At each point record, a pin of 5 mm diameter taller than the

162   maximum height of the vegetation was projected from above, and all contacts were recorded

163   if the pin hit any of the live parts of a grass species. The positions of the transect lines were

164 permanently marked to ensure accurate relocation each year. Identification of species and

165 families of plants follows Hutchinson et al. (1954).

166

167 Initial data exploration to investigate the range of variation in the data set was carried out

168 using detrended correspondence analysis (DCA), a method of indirect gradient analysis (ter

169 Braak and Smilauer, 2002). However, the gradient length for the first axis was 1.05 and 1.33

170 for Tiogo and Laba, respectively, which are less than the recommended values, 3.0; thus

171 species data set was ordinated with Principal Component Analysis (PCA). The abundance

172 data for all herbaceous species (152 and 176 at Tiogo and Laba respectively) in response to

173 fire, grazing, selective cutting and their interactions over the study period were then analyzed

174 using Principal Response Curves (PRC) analysis. This technique is based on the ordination

175 technique called partial redundancy analysis and developed specifically for analysis of

176 community response data from designed experiments sampled repeatedly through time (van

177 den Brink and ter Braak, 1998; 1999). Time coded as dummy variable was considered as

178 covariable and only time by treatment interaction (also coded as dummy variable) were

179 considered as explanatory variables. PRC plots the first principal component of the treatment

180 effects against time, expressed as deviations from the control/reference treatment (van den

181 Brink and ter Braak, 1998). The general model for the first principal component can be

182 expressed as:

183 $\quad Y_{d(j)tk} = \overline{Y}_{0tk} + b_k c_{dt} + \varepsilon_{d(j)tk}$

184 where $Y_{d(j)tk}$ is the abundance of species k in replicate j of treatment d at year t, $\overline{Y}_{0tk}$ is the

185 mean log-abundance of species k in year t in the control ($d = 0$), c_{dt} is the score of the dth

186 treatment at year t, d_k is the weight of the kth species and $\varepsilon_{d(j)tk}$ is an error term with mean

187   zero and variance σ_k^2. The coding used in the PRC standardized the control to be zero-valued

188   ($C_{ot} = 0$) for all times i.e. horizontal line in the PRC diagram. Species abundance was

189     $\ln(x+1)$-transformed to approximate the normal distribution while accounting for large

190   number of zeros in the initial species data matrices, for which ln0 is undefined. In this case the

191   reference (the control) was taken as the no fire + no cutting + no grazing plots. The

192   underlying assumption for choosing this treatment as reference was that a system in

193   undisturbed state is fairly stable and the effect of any disturbance can be gauged against this

194   stable state. Associated with each PRC is a set of species weights, which reflect the influence

195   of particular species on the overall community response described by the PRC scores over

196   time. Species with high positive scores are positively correlated, species with negative scores

197   respond oppositely, and species with near-zero scores are indifferent to the trend recognized

198   by the PRC axes (ter Braak and Smilauer, 2002). The statistical significance of the resulting

199   PRC axes was evaluated using Monte Carlo permutation tests (p < 0.05 after 499

200   permutations under split-plot constraints) by permuting freely data from the whole treatments

201   within each year. Changes in treatment effects through time were evaluated in sequential tests

202   for each sampling year by permuting the census data. Monte Carlo permutation test was also

203   performed to determine the effects of each treatment separately in time, plus their interactions

204   with other treatments. The statistical analyses were performed using the software package

205   CANOCO 4.5 and the ordination diagrams drawn in CANODRAW (ter Braak and Smilauer,

206   2002).

207

208   **3. Results**

209   The initial ordination of the herbaceous vegetation using PCA showed a low degree of

210   variation in the abundance of species between treatments averaged over the study period, as

211   evidenced from the low eigenvalue for the first axis, which was 0.34 for Tiogo and 0.41 for

212   Laba. The PCA score/loading biplot further showed a low affinity of species to particular

213   treatment at both Tiogo (Fig. 3A) and Laba (Fig. 3B). Although species affinity to treatments

214   appeared low, it was still difficult to visualize, quantify and test for treatment by year

215   interactions within the classic ordination framework provided by PCA. It should be noted that

216   we averaged the abundance across the study years in order to clearly see how the responses of

217   individual species spread over the different treatments.

218

219   The PRC ordination accounted for 38% and 34% of the variation within the data set for Tiogo

220   and Laba, respectively (Table 1). The PRC models for the first axis in the full data showed

221   that 13% and 8% of the total variation were attributed to sampling years at Tiogo and Laba,

222   respectively while treatment regime accounted for 25% and 26% of the total variation at

223   Tiogo and Laba, respectively (Table 1). At both study sites, the first axis captured 25% to

224   35% of the total variation and was significant (Table 1). The second axis was also significant

225   for Tiogo but not for Laba. The effects of each treatment separately in time, plus their

226   interactions with other treatment indicated that the variation accounted for by the first axis

227   ranged from 55% to 72% at Tiogo and 23% to 79%.at Laba (Table 1). At Tiogo, the first PRC

228   axis was significant for all treatments and their interactions except grazing and fire × cutting

229   treatment, while at Laba it was significant for cutting, fire × grazing and fire × cutting ×

230   grazing treatments. The PRC diagram for the first axis showed that there were two directions

231   of departure from the control plots at Tiogo where fire, grazing and selective cutting were not

232   applied (Fig. 4A). The main effects of fire, selective cutting and grazing on abundance were

233   generally positive for the herbaceous vegetation community through out the study period;

234   particularly these treatments favoured species, such as *Loudetia togoensis*, *Andropogon*

235   *fastigiatus*, and *Andropogon pseudapricus*. The interaction effects were generally negative at

236   community level compared to the control across the study period while having pronounced

237   positive effects on species such as *Andropogon gayanus, Chasmopodium caudatum* and

238   *Andropogon ascinodis*. Several species had their weight close to zero, indicating that they

239   seemed insensitive to the treatments over time. The Monte Carlo tests per sampling year

240   revealed that the treatment regimes had significant effects on herbaceous species abundance

241   after 4 (1998), and 6-10 (2000-2004) years (Table 2). The PRC diagram also showed that the

242   extent of the fire, selective cutting, and fire × cutting × grazing interaction effects was larger

243   than the effects of grazing and other interactions as evidence from the large deviation of these

244   lines from the control (Fig. 4A).

245

246   For the second axis, the PRC diagram revealed additional treatment effects as evidenced from

247   a new set of species (Fig. 4B). The extent of fire and selective cutting main effects was larger

248   than the oppositely oriented main effect of grazing, shown by the lines directed to the

249   negative side of the vertical axis. Apparently, fire enhanced the abundance of *Andropogon*

250   *ascinodis* and *Diheteropogon amplectens* throughout the study period, so also selective

251   cutting during most of the study period. Among treatment interactions, cutting × grazing and

252   fire × cutting × grazing had a larger positive influence on the abundance of species such as

253   *Pennisetum pedicellatum* during most of the study period. Several other species also

254   responded differentially to treatments during the study period as shown by their weights.

255

256   At the second case study site, Laba, the PRC analysis for the first significant axis revealed

257   that the treatment effects over time deviated from the control bi-directionally where the main

258   effects of fire, grazing and selective cutting are oriented in the negative side of the vertical

259   axis while the interaction effects are oppositely oriented except grazing × cutting (Fig. 5). Fire

260   strongly influenced the abundance of herbaceous species during the study period by favoring

261   species such as *Elionurus elegans, Andropogon fastigiatus, Diheteropogon hagerupii* and

262   *Loudetia togoensis* while disfavoring *Andropogon gayanus, Schizachyrium sanguineum,*

263   *Andropogon ascinodis* and *Monocymbium ceresiiforme*. Grazing was the second most

264   important factor affecting the abundance of herbaceous species over time followed by

265   selective cutting. The extent of influence exerted by treatment interactions was generally

266   small compared to main effects of fire and grazing. On the basis of Monte Carlo tests per

267   sampling year, the treatment regimes had significant effects on herbaceous species abundance

268   after 8-12 years (2002-2006) while marginally significant after 5 (1999) and 7 (2001) years

269   (Table 2).

270

271   Summary of the test for each treatment effect over time for Tiogo is presented in Table 2A,

272   and the pattern is graphically depicted in Fig. 4A. The main effect of fire was significant in

273   2002 where abundance of herbaceous vegetation was relatively low compared with the

274   previous sampling years. The effect of grazing was significant during the last five years of

275   sampling (2002-2006) where abundance was higher in these sampling years except 2003

276   when grazing resulted in reduced abundance compared to the other sampling years. Selective

277   cutting had more positive effect on the abundance of herbaceous vegetation community in

278   1997, 1998 and 2004 than the rest of the sampling years. The interaction effect of fire ×

279   cutting was positive in 1994 and 2003 than the other sampling years when abundance was

280   relatively lower than the control. The fire × grazing treatment had a decreasing effect on

281   abundance for the sampling years 2001, 2003 and 2005 and an increasing effect in 2004. The

282   abundance of the herbaceous vegetation generally decreased in cutting × grazing and fire ×

283   grazing × cutting plots through out the sampling years except 2003 in the former and in 2002

284   and 2003 in the latter when abundance was closer to the control.

285

286   Similar Monte Carlo tests results for the second case study site, Laba, is given in Table 2B,

287   and the pattern of this inter-annual variation depicted in Fig. 5. The fire treatment resulted in

288   significantly lower abundance in 2001 than in some of the sampling years (e.g. 1994, 1997,

289   2005), while grazing reduced the abundance of herbaceous vegetation during the last three

290   years (2004-2006) compared with the previous years. The effects of selective cutting did not

291   vary across sampling years. In fire × grazing treatment, the response of herbaceous vegetation

292   was positive in 1995, 1998 and 2001-2006 while negative in 1994 and 1999. Abundance was

293   lower in 2004 for fire × cutting treatment, in 2002-2006 for cutting × grazing and in all

294   sampling years except 1995-1997 for fire × grazing × cutting treatment than the other

295   sampling years.

296

297   **4. Discussion**

298   *4.1 PRC model overview*

299   The PRC model summarized the extensive species by sample data with one or two significant

300   axes, depending on the case study site. Dimensional complexity is an important factor in the

301   interpretation of multivariate analysis and models with few dimensions (axes) are often highly

302   preferred. The proportion of variation accounted in the PRC ordination was higher for the

303   treatment regime (involving time by treatment interaction) than for time for both study sites.

304   This suggests that the treatment effects on species abundance were more important than the

305   time per se. The fact that more than one PRC axis was needed to summarize the large data set

306   from Tiogo suggests that the species reacted in quantitatively different ways to the treatments,

307   as can be deduced from their weights.

308

309   *4.2 Responses to individual treatments*

310   The species composition of savanna ecosystems is maintained by a dynamic interaction

311   between local colonization and local extinction due to competitive exclusion. In turn, these

312   are influenced by disturbances, such as fire, herbivory and selective cutting (Breman and

313   Kessler, 1995; Gibson and Brown, 1991; McNaughton, 1983). At the Tiogo study site, the

314   effect of fire, selective cutting or grazing on the perennial grasses *Andropogon gayanus,*

315   *Andropogon ascinodis* and *Schizachyrium sanguineum* in the herbaceous vegetation

316   community was negative compared to the control, but not for the annual grass *Chasmopodium*

317   *caudatum*. On the deep soils of Tiogo, these treatments tended to favour annual grass species

318   and adversely affect perennial ones. Low intensity fire (such as early fire) enhances the

319   colonization processes by inducing a flush of germination and flowering, a transient increase

320   in overall productivity due to removal of litter that increases the availability of nutrients,

321   space and light, as well as maintaining tussocks and increasing their cover by favouring the

322   tillering of perennial grass (Garnier and Dajoz, 2001; Whelan, 1995). In contrast, recurrent

323   fires may create unfavourable conditions for the germination of some species and can exhaust

324   the below-ground reserves of perennials leading to their disappearance and replacement with

325   more competitive annuals. In addition, post fire gaps may be drought-prone as a result of

326   elevated evaporation that reduces moisture availability at the shallow depths where

327   germination occurs, thus contributing to extinction processes (Elberse and Breman, 1990).

328   The opposite effect was noted at the Laba study site: in the shallow soils at this site the

329   perennial grass species *Andropogon gayanus, Schizachyrium sanguineum, Andropogn*

330   *ascinodis, Monocymbium ceresiiforme* were favoured by the treatments while the annual grass

14

331 species were adversely affected. The inter-site variability in the fire effect could be due to the

332 occurrence of only short-lived fires at Laba because of the dominance of annual grass species

333 with lower biomass compared to Tiogo where perennials dominate. The inter-site variability

334 in fire effect could be due to relatively high fire intensity at Laba, which, in turn, is related to

335 the increased availability of fuel in the form of biomass from annual grasses.

336

337 During the first half of the study period (1994-1999), the abundance of herbaceous vegetation

338 increased somehow steadily in response to fire treatment, particularly at Tiogo. This initial

339 increase may be related to increased availability of nitrogen and other nutrients essential for

340 plant growth through deposition of ash (Jensen et al., 2001; Wan et al., 2001). The treatment

341 effect was statistically significant (Monte Carlo tests) for 2001 at Laba and 2002 at Tiogo,

342 which could be explained by interaction of fire with other environmental factors, such as

343 rainfall. The mean annual rainfall was low for three consecutive years (2000-2002) at both

344 study sites compared to the immediate sampling years before and after these years. Fire

345 treatment might exacerbate drought in the post burn environment and resulted in reduced

346 abundance of herbaceous vegetation. As a whole, the effect of fire on herbaceous vegetation

347 community depends on growth form, fire frequency and intensity (Bennett et al., 2003;

348 Sawadogo et al., 2005), and the latter in turn depends on fuel load, moisture content of the

349 fuel and weather conditions (Goldammer, 1990; Scholes and Walker, 1993).

350

351 The species composition and abundance of the understory increases following the formation

352 of canopy gaps created by tree removal; this is due to reduced competition for water and

353 nutrients as well as increased availability of light and growing space (Akpo et al., 2003; Frost

354 et al., 1986). There is evidence of this in the first PRC diagram for the Tiogo study site, where

355 abundance increased steadily during the first five years of the study period. In contrast, at

356 Laba the effect of selective cutting on the abundance of herbaceous vegetation over time was

357 slightly negative. This could be related to drought effects, exacerbated by the selective

358 removal of trees at Laba where the soil is mainly shallow, silty-sand with a low water holding

359 capacity. It is indeed expected that the canopy gaps created by selective removal of trees may

360 create unfavourable thermal conditions in arid and semi-arid areas and favour the growth of

361 drought-tolerant species only, thereby contributing to competitive exclusion process.

362

363 Although grazing had a positive effect on the herbaceous vegetation community during the

364 study period, the extent of its effect was lower than that of fire or selective cutting at Tiogo.

365 The grazing intensity in our subplots, particularly at Tiogo, was half the carrying capacity

366 (Sawadogo, 1996), thus many species could survive intermediate levels of grazing that allows

367 succession to proceed but limits the ability of a few highly competitive species to dominate

368 the community. Generally, moderate grazing enhances plant diversity through enhanced

369 propagule dispersal, increased availability of light, and improving soil conditions while

370 reducing local extinction rates by preferentially consuming competitive, dominant plants (Olff

371 and Ritchie, 1998). The dynamics of grazing effects during the course of the study period are,

372 in fact, related to the spatio-temporal variation in stocking rate and grazing intensity, which

373 are common in the Sahel region (Hiernaux, 1998). At Laba, grazing had a greater negative

374 impact at community level during the study period. This negative effect could be a

375 consequence of the low biomass production at this site (Sawadogo et al., 2005) coupled with

376 heavier grazing pressure (Sawadogo, 1996) than at Tiogo.

377

378 *4.3 Responses to treatment interactions*

379 Generally all treatment interactions had a negative effect on the herbaceous vegetation

380 community at Tiogo site during most of the study period. Their effects, however, were

16

381 positive (increasing abundance) for perennial grass *Andropogon gayanus, Andropogon*

382 *ascinodis* and *Schizachyrium sanguineum.* The fire × cutting × grazing treatment effect was

383 more pronounced than the other interaction effects. The removal of trees in 1994 created more

384 growing space and probably enhanced the abundance of herbaceous vegetation. The increased

385 availability of forage, in turn, might attract more herbivores and/or resulted in intense fire that

386 eventually decreased the abundance of herbaceous species. The negative effect of this

387 treatment interaction slightly fluctuated across the sampling years until 2002 and 2003 when

388 abundance increased significantly closer to the control. This dynamics can be explained by

389 the gradual decrease in the positive effect of selective cutting (increased growing space and

390 reduction of competition) due to rapid colonization during the first few years (as can be seen

391 from steady-state increase in selectively cut plots), which in turn reduced the availability of

392 fuels and fire intensity. From the PRC diagram (Fig. 4A) it appears that the extent of selective

393 cutting × grazing effect was more pronounced than the effect of fire × cutting or fire ×

394 grazing. This indicates high grazing pressure and stocking rate in response to abundance of

395 forage following selective removal of trees, which might be the reason for limited effect of

396 this treatment over the study period. Contrary to Tiogo, treatment interactions resulted in

397 higher abundance of herbaceous vegetation community relative to the control during most of

398 the study years, except cutting × grazing treatment. This site-specificity could be partly

399 explained by the spatial distribution of herbaceous species at each case study site. At Laba, 12

400 dominant species responded positively for treatment combinations than 4 dominant species at

401 Tiogo (c.f. Fig. 4A and 5).

402

403   *4.4 Methodological importance*

404   Analysis of large scale studies on disturbance dynamics is often centred around the use of

405   conventional statistical methods, such as analysis of variance (Sawadogo et al., 2005) or

406   repeated measures analysis (Savadogo, 2007) based on data pooled over time or data from just

407   a few individual species. Such analyses fail to reflect how the effects of disturbance vary over

408   time or they do not allow the interpretation of results simultaneously at both community and

409   individual species levels. PRC is a method for the visualization of results of repeated

410   measurements analysis, focusing on time-dependent treatment effects (van den Brink and ter

411   Braak, 1998; 1999). It has the capacity to reveal trends at a major community level within a

412   large data matrix, combined with an increased ecological relevance to studies at lower levels

413   of biological organization (Kedwards et al., 1999). PRC analysis has been successfully used

414   in a variety of applications ranging from ecotoxicological field studies (Kedwards et al., 1999;

415   van den Brink and ter Braak, 1998; 1999), climate change effects (Frampton et al., 2000;

416   Heegaard and Vandvik, 2004; Vandvik, 2004), vegetation and disturbance dynamics (Britton

417   and Fisher, 2007; Francisco et al., 1995; Kohler et al., 2006; Pakeman, 2004; Pakeman et al.,

418   2003; Vandvik, 2004; Vandvik et al., 2005) to the effects of ecosystem type (Neher et al.,

419   2005) and agricultural management regime (Salles et al., 2006). In all these applications PRC

420   appears to be a powerful tool for analyzing community responses to different perturbations

421   over time than the conventional univariate methods and multivariate ordination techniques

422   (e.g. DCA). Compared to our previous results based on repeated measures analysis of

423   variance (Savadogo, 2007), PRC enabled us to interpret treatment effects not only at the

424   community level but also at the individual species level. Such information is indispensable for

425   identifying species that can serve as indicators of particular disturbance regimes. For example,

426   Leps & Smilauer (2003) demonstrated the potential value of multivariate methods for

427   identifying indicator species or taxa, the abundance of which may be indicative of particular

428 environmental variables or experimental treatments. Since species with the highest weights in

429 PRC analysis are most likely follow the overall community response, species weight may be

430 used to identify potential indicator species. In our study, *L. togoensis*, *A. gayanus*, *A.*

431 *fastigiatus*, *A. ascinodis*, *C. caudatum* and *Pennisetum pedicellatum* have the highest weights

432 at Tiogo, while *A. gayanus*, *A. fastigiatus*, *Elionurus elegans* and *Schizachyrium sanguineum*

433 have the highest weights at Laba. Thus, these species could potentially serve as indicators of

434 fire, grazing and selective cutting disturbances in the Sudanian savanna woodland. The

435 limitations of this technique should be mentioned as well. This method assigns a single

436 weight to each species suggesting that their relative importance does not change over time

437 contrary to the fact that the treatments applied in this experiment may generate processes with

438 changing nonlinear contributions (weights) of species.

439

440 **Conclusions**

441 This study illustrates that the herbaceous vegetation component of savanna-woodland

442 responds differently along a time gradient to single or combined disturbances of fire, grazing

443 and tree removal. Furthermore these effects are site-specific, suggesting that their effects

444 interact with other environmental factors such as soil characteristics. The dynamics of these

445 disturbance regimes also interact, to some extent, with rainfall. The PRC approach to the

446 analysis of disturbance dynamics in this study appears to be indispensable, in that it allows

447 identification of potential indicator taxa that could be used for monitoring the effects of

448 disturbance regimes on the herbaceous community in savanna-woodlands.

449

450 **Acknowledgements**

19

456 **Appendix.** Names and growth form (Pe= perennial grass, An =annual grass, Fb= forbs) of the

457 species considered in Detrended Correspondence Analysis (DCA) at Tiogo and Laba

Species	Code	GF	Family
Andropogon ascinodis C. B. Cl.	Anas	Pe	Poaceae
Andropogon fastigiatus Sw.	Anfa	An	Poaceae
Andropogon gayanus Kunth	Anga	Pe	Poaceae
Andropogon pseudapricus Stapf	Anps	An	Poaceae
Aspilia bussei O. Hoffm. Et Muschl.	Asbu	Fb	Asteraceae
Blepharis maderaspatensis (L.) Heyne ex Roth	Blma	Fb	Acanthaceae
Borreria radiata DC.	Bora	Fb	Rubiaceae
Borreria scabra DC.	bosc	Fb	Rubiaceae
Borreria stachydea DC.	Bost	Fb	Rubiaceae
Brachiaria distichophylla (Tri) Stapf	Brdi	An	Poaceae
Chasmopodium caudatum (Hack.) Stapf	Chca	An	Poaceae
Chlorophytum senegalense (Bak.) Hepper	Chse	Fb	Liliaceae
Cochlospermum planchoni Hook. F.	Copl	Fb	Coclospermaceae
Cymbopogon schoenanthus Mair & Weiller	Cysc	Pe	Poaceae
Digitaria horizontalis Wild.	Diho	An	Poaceae
Diheteropogon amplectens (Nees) W.D. Clayton	Diam	Pe	Poaceae
Diheteropogon hagerupii Hitchc.	Diha	An	Poaceae
Elionurus elegans Kunth	Elel	An	Poaceae
Euclasta condylotricha (Hochst ex Steud.) Stapf	Euco	An	Poaceae
Hackelochloa granularis (L.) O. Ktze.	Hagr	An	Poaceae
Hoslundia oppositaVahl	Hoop	Fb	Lamiaceae
Kaempferia aethiopica (Schweinf.) Solm-Laub.	Kaae	Fb	Zingiberaceae
Loudetia togoensis (Pilg.) Hubb.	Loto	An	Poaceae
Microchloa indica Beauv.	Miin	An	Poaceae
Pandiaka heudelotii (Moq.) Hook.	Pahe	Fb	Amaranthaceae
Pennisetum pedicellatum Trin	Pepe	An	Poaceae
Pennisetum polystachion (Linn.) Schult.	Pepo	An	Poaceae
Rhytachne triaristata (Steud.) Stapf	Rhtr	An	Poaceae
Rottboellia exaltata Linn..	Roex	An	Poaceae
Schizachyrium exile (Hochst.) Pilger	Scex	An	Poaceae
Schizachyrium sanguineum (Retz.) Alston	Scsa	Pe	Poaceae
Sorghastrum bipennatum (Hack.) Pilger	Sobi	An	Poaceae
Tephrosia pedicellata Bak.	Tepe	Fb	Fabaceae
Tripogon minimis Hoschst. ex Steud.	Wiam	Pe	Poaceae

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Table 1. Percentage of the total variance that can be attributed to time and treatment regime within the data sets collected at Tiogo and Laba experimental sites. The treatment regime includes the interaction between treatments and time. The remaining fraction of variance is residual variance. The fractions of variance explained by the treatment regime that are captured by the first and second Principal Response Curves are also presented.

A. Tiogo

	Full data set	Data subset						
		F	G	C	F x G	F x C	C x G	F x C x G
Variance accounted for by								
Time	13	19	23	19	25	20	25	23
Treatment regime	25	18	15	19	17	25	12	15
Explained variance captured by								
First PRC	25*	58*	61	65*	58*	72	55*	63*
Second PRC	21*	26	27	29	33	31	25	23

B. Laba

	Full data set	Data subset						
		F	G	C	F x G	F x C	C x G	F x C x G
Variance accounted for by								
Time	8	8	13	16	10	10	12	11
Treatment regime	26	20	17	11	25	16	18	30
Explained variance captured by								
First PRC	35*	23	65	54*	75*	68	69	79*
Second PRC	20	1	27	16	25	25	25	1

* Significant axes (p < 0.05); F: Fire; G: Grazing; C: Cutting

Table 2. Summary of the Monte Carlo permutation tests (number of permutation 499) of PRC axes 1 and 2, and sequential tests on data subsets for each treatment separately in time.

A. Tiogo

	Full data set	Data subsets						
		F	G	C	F x G	F x C	C x G	F x C x G
All canonical axes	0.247*	0.182*	0.150	0.194*	0.170*	0.246	0.115	0.153*
PRC axis 1	0.062*	0.106*	0.091	0.127*	0.098*	0.178	0.063*	0.097*
PRC axis 2	0.039*	0.020	0.016	0.019	0.024	0.021	0.013	0.013
1994	0.060	0.117	0.115	0.081	0.146	0.074	0.068	0.113
1995	0.092	0.251	0.185	0.325	0.127	0.336*	0.159	0.129
1996	0.104	0.269	0.150	0.277	0.183	0.324*	0.129	0.125
1997	0.109	0.198	0.131	0.281*	0.155	0.314*	0.116	0.134
1998	0.133*	0.232	0.134	0.280*	0.208	0.278*	0.136	0.154
1999	0.105	0.207	0.184	0.214	0.142	0.270*	0.172	0.174
2000	0.155*	0.303	0.145	0.288	0.204	0.308*	0.162	0.176
2001	0.153*	0.289	0.186	0.289	0.317*	0.462*	0.116	0.190
2002	0.118*	0.281*	0.246*	0.248	0.252	0.395*	0.168	0.368*
2003	0.131*	0.185	0.269*	0.156	0.322*	0.237	0.259*	0.239*
2004	0.102*	0.252	0.231*	0.243*	0.292*	0.360*	0.175	0.238
2005	0.099	0.216	0.282*	0.239	0.332*	0.356*	0.143	0.282
2006	0.091	0.159	0.239*	0.212	0.236	0.300*	0.154	0.188

* Significant eigenvalue (p < 0.05); F: Fire; G: Grazing; C: Cutting

B. Laba

	Full data set	Data subset						
		F	G	C	F x G	F x C	C x G	F x C x G
All canonical axes	0.257*	0.179	0.168	0.106	0.253	0.164	0.180	0.295
PRC axis 1	0.089*	0.123	0.110	0.057*	0.189*	0.112	0.125	0.232*
PRC axis 2	0.033	0.013	0.016	0.008	0.016	0.013	0.014	0.019
1994	0.054	0.129	0.156	0.103	0.156	0.116	0.148	0.099
1995	0.093	0.199	0.147	0.129	0.249*	0.125	0.175	0.241
1996	0.095	0.154	0.202	0.093	0.220	0.136	0.195	0.268
1997	0.079	0.139	0.120	0.123	0.209	0.118	0.150	0.210
1998	0.116	0.200	0.175	0.150	0.271*	0.156	0.151	0.325*
1999	0.120*	0.276	0.184	0.210	0.346*	0.259	0.214	0.311
2000	0.133	0.203	0.191	0.125	0.272	0.221	0.231	0.413*
2001	0.138*	0.240*	0.166	0.135	0.264*	0.240	0.205	0.405*
2002	0.119	0.231	0.205	0.127	0.304*	0.171	0.255*	0.344*
2003	0.139*	0.199	0.197	0.084	0.296*	0.164	0.208*	0.392*
2004	0.165*	0.238	0.264*	0.117	0.400*	0.260*	0.234	0.426*
2005	0.145*	0.187	0.262*	0.116	0.342*	0.202	0.245*	0.393*
2006	0.166*	0.266	0.242*	0.136	0.327*	0.234	0.244*	0.488*

* Significant eigenvalue (p < 0.05); F: Fire; G: Grazing; C: Cutting

Figures captions

Fig. 1. Annual rainfall and number of rainy days for Tiogo and Laba across the study period.

Fig. 2. Lay-out of the factorial experimental design.

Fig. 3. PCA biplots of an ordination of species by treatment regimes for two case study sites (A for Tiogo and B for Laba). A complete list of species is given in the appendix and the treatment regimes abbreviated as follows: F = fire, G = grazing, C = selective cutting, FG = fire × grazing, FC = fire × cutting, CG = cutting × grazing, FGC = fire × grazing × cutting.

Fig. 4A. PRC score plots together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and their interactions over 13 years at Tiogo site: A) PRC axis 1. Only species with relatively strong responses are shown for the sake of clarity.

Fig. 4B. PRC score plots together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and their interactions over 13 years at Tiogo site: B) PRC axis 2. Only species with relatively strong responses are shown for the sake of clarity.

Fig. 5. PRC score plot together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and their interactions over 13 years at Laba site. Only species with relatively strong responses are shown for clarity.
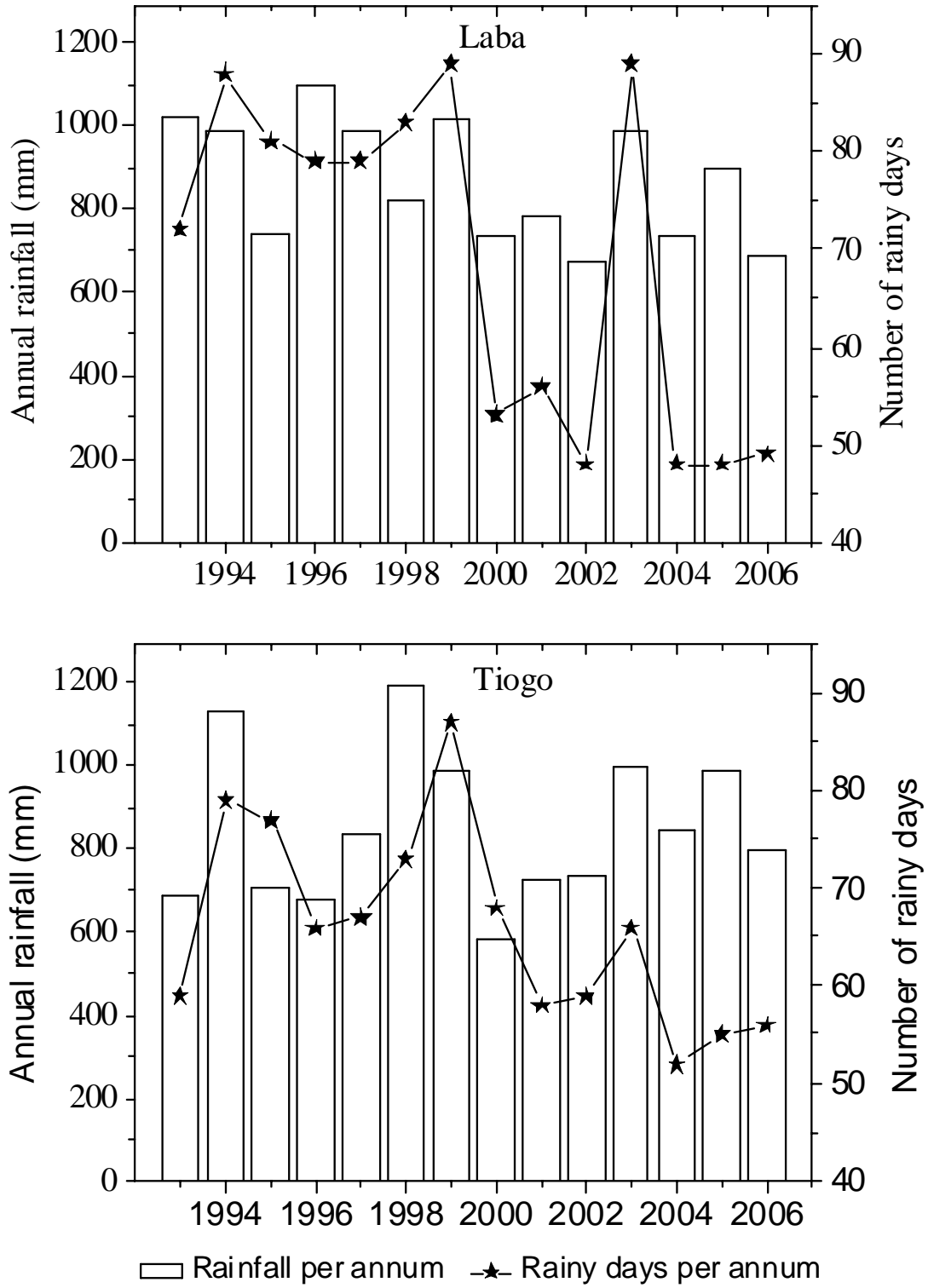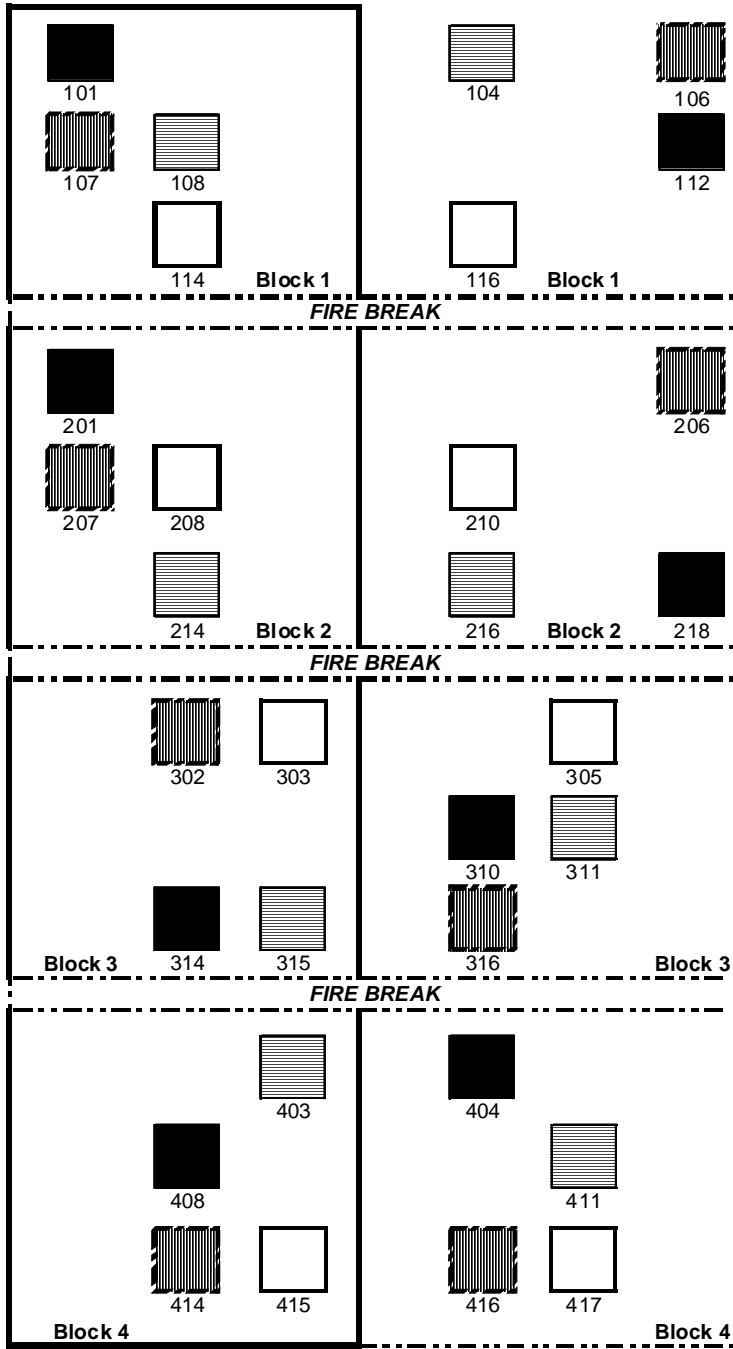
Fig. 1.

Fig. 2.

Block 1   101   107   108   114   Block 1   104   106   112   116

FIRE BREAK

Block 2   201   207   208   214   Block 2   206   210   216   218

FIRE BREAK

Block 3   302   303   314   315   Block 3   305   310   311   316

FIRE BREAK

Block 4   403   408   414   415   Block 4   404   411   416   417

Legend

Annual Fire + No Cutting   No Fire + No Cutting

Annual Fire + Cutting   No fire + Cutting

Livestock exclosure

Fig. 3.

Fig. 4A.

Legend:
◆ Fire; ○ Grazing; ✧ Cutting; ▶ Fire x Cutting;
■ Grazing x Cutting; ▬ Fire x Grazing; ● Fire x Cutting x Grazing

X-axis: Sampling years (1994–2006)
Y-axis (left): PRC1 (−0.6 to 0.6)
Y-axis (right): Species weight (axis 1) (−6.0 to 8.0)

Species (right panel, top to bottom):
Loudetia togoensis
Andropogon fastigiatus
Andropogon pseudapricus
Euclasta condylotrichia
Microchloa indica
Hoslundia opposita
Ampelocissus grantii
Cymbopogon schoenanthus
Kalanchoe crenata
Brachiaria lata
Tephrosia bracteolata
Cochlospermum tinctorium
Schizachyrium sanguineum
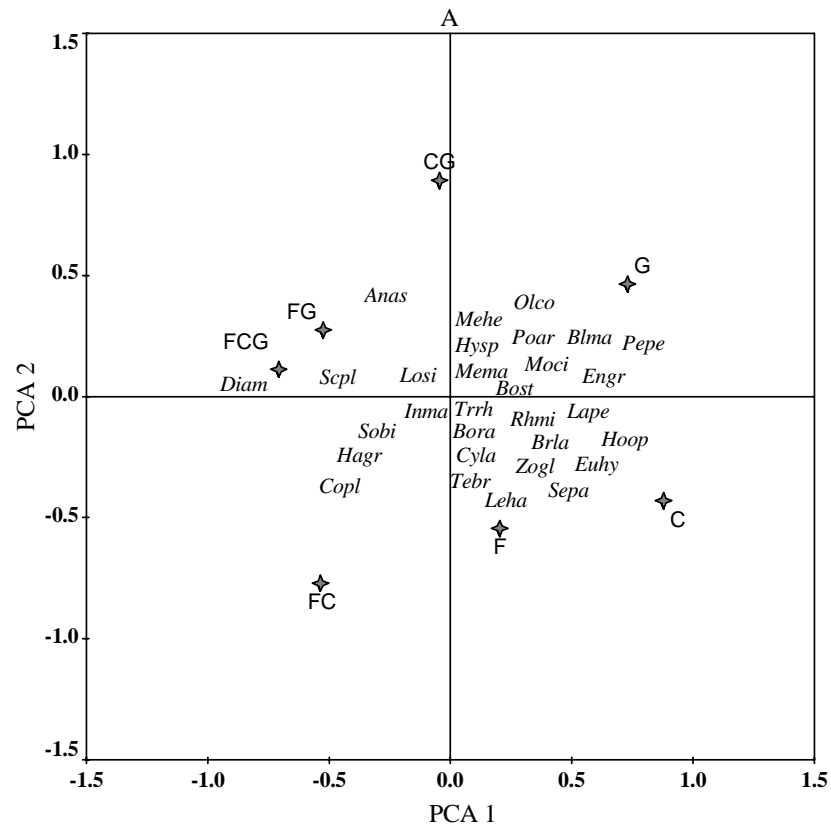*Andropogon ascinodis*
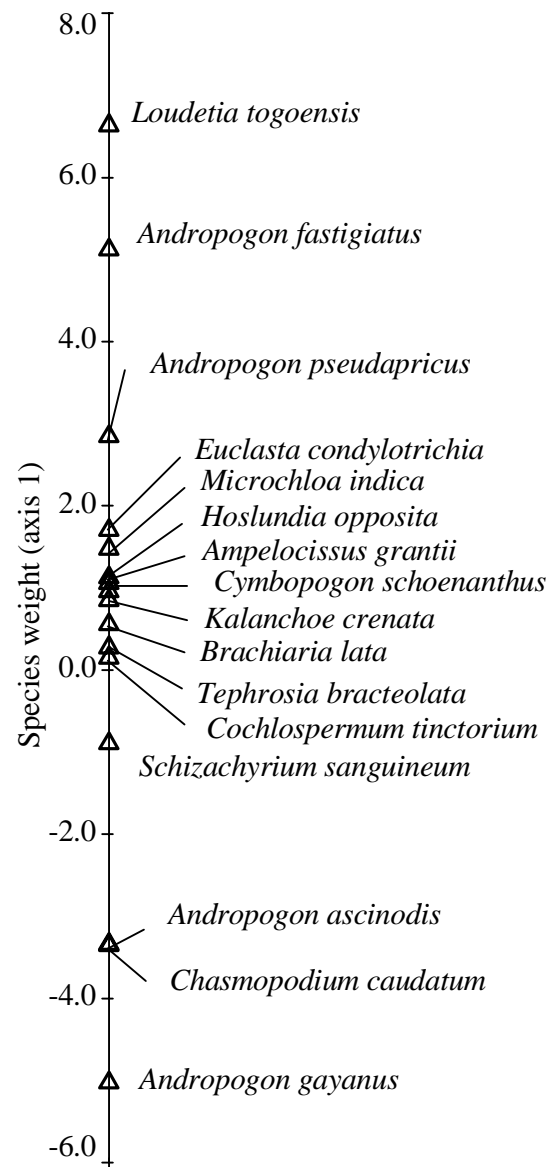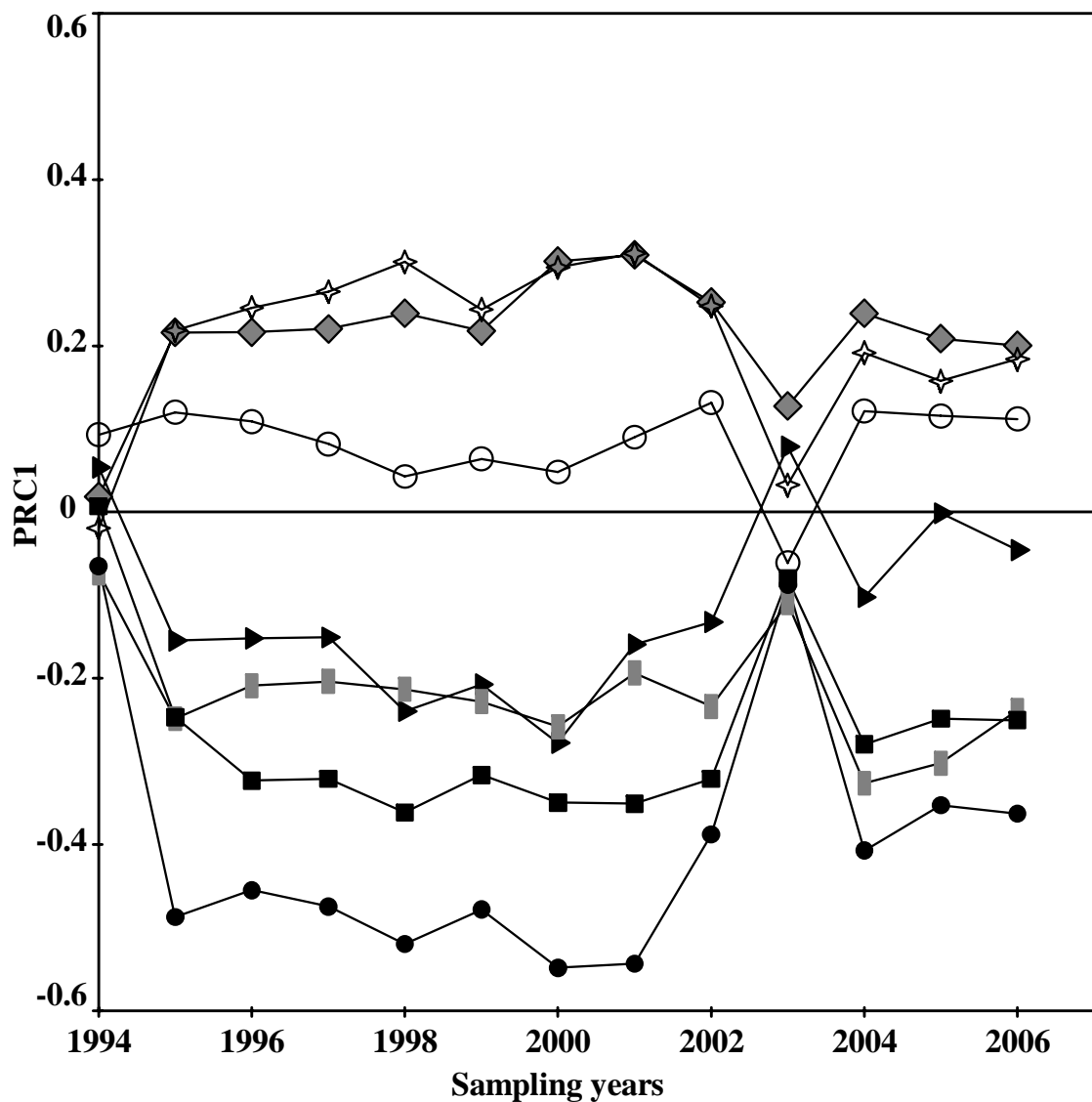*Chasmopodium caudatum*
Andropogon gayanus

Fig. 4B.

Fire; ○ Grazing; ◇ Cutting; ▶ Fire x Cutting;

■ Grazing x Cutting; ▮ Fire x Grazing; ● Fire x Cutting x Grazing

Fig. 5.

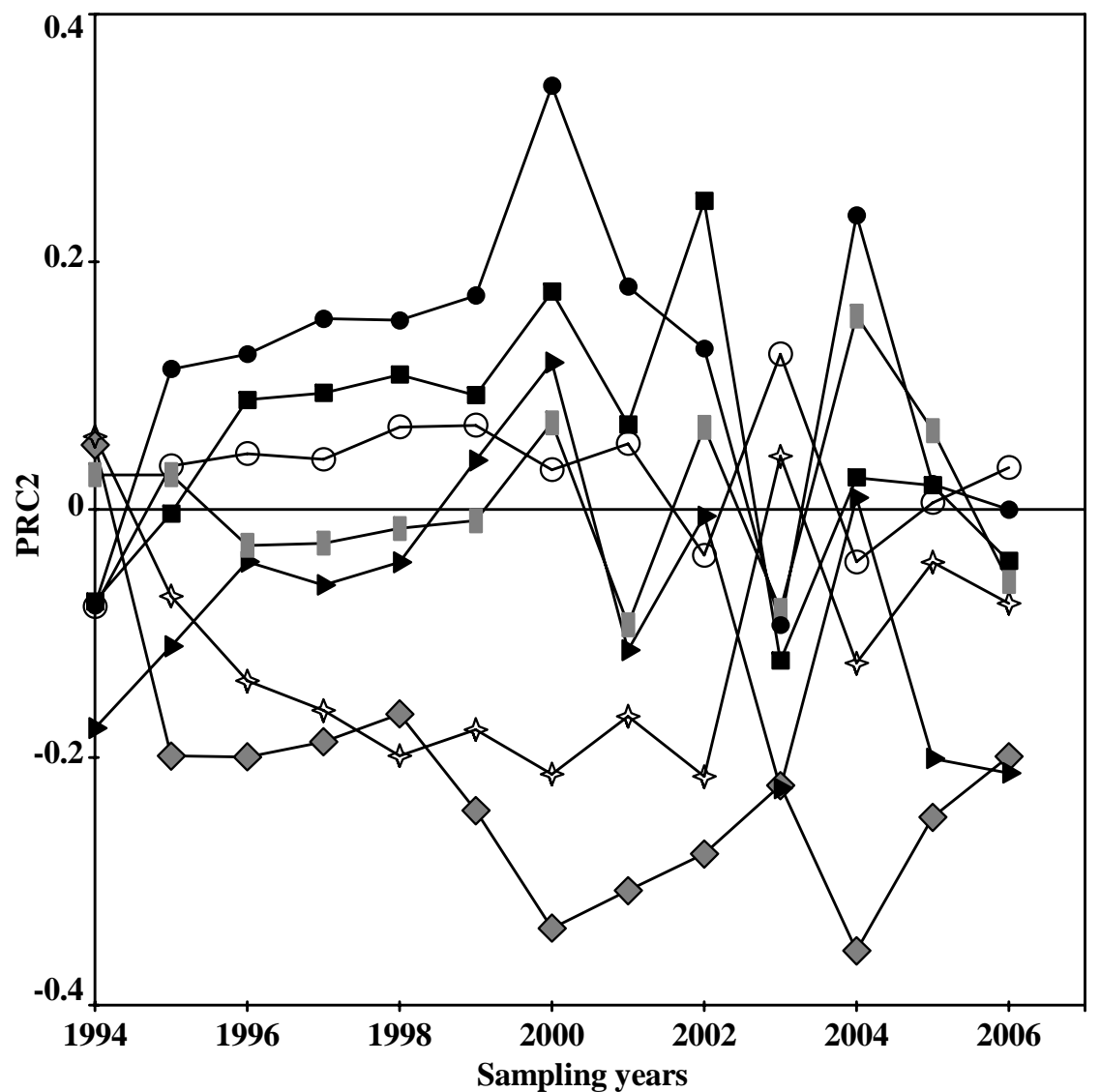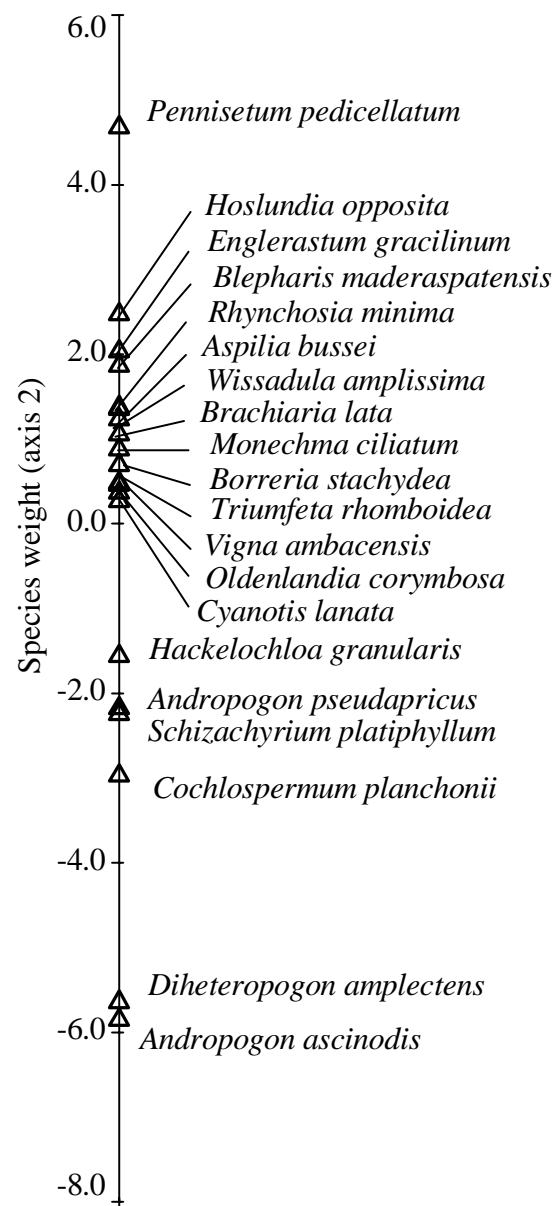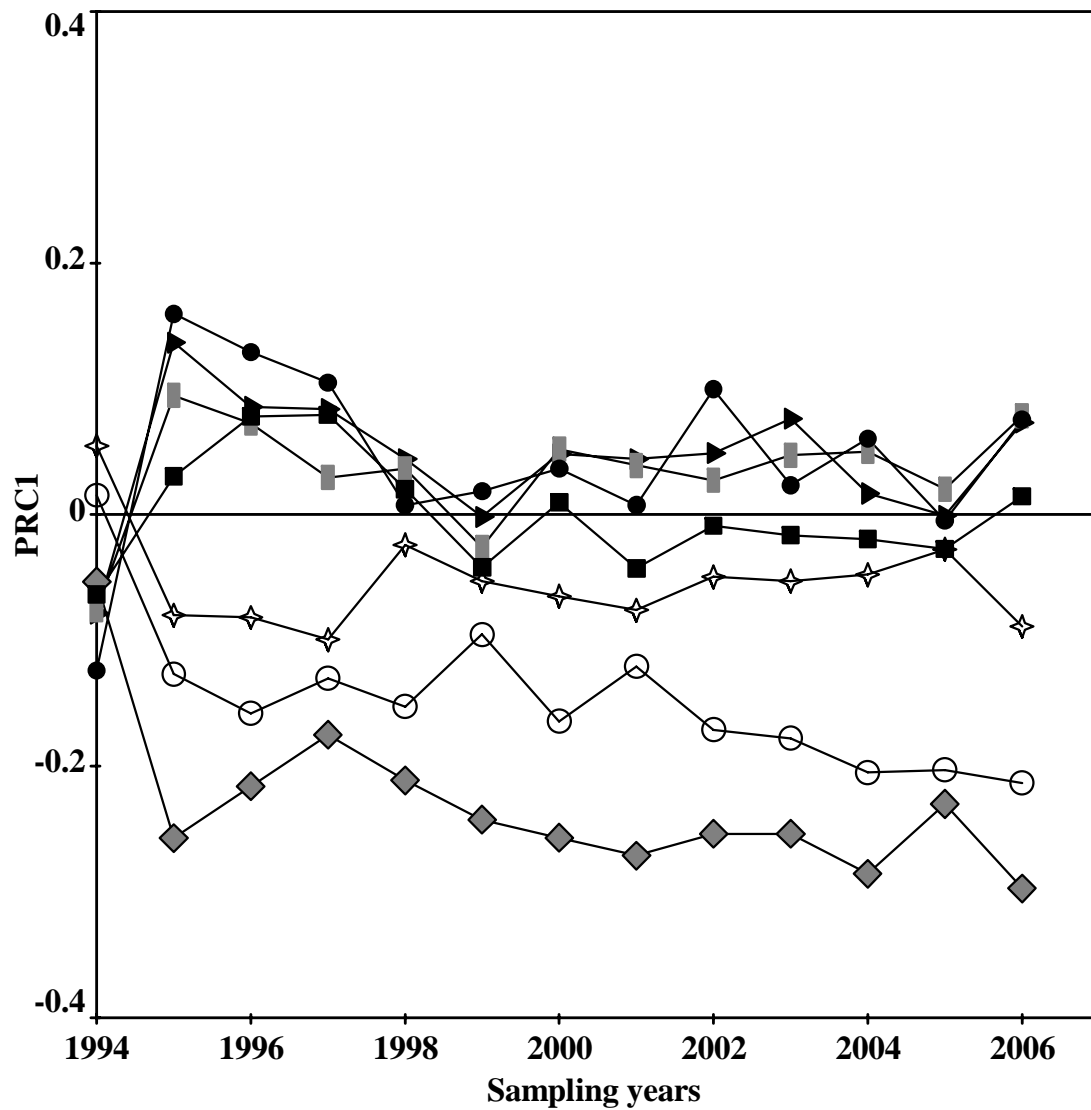Legend (x-axis: Sampling years; y-axis left: PRC1; y-axis right: Species weight (axis 1)):

◆ Fire; ○ Grazing; ✧ Cutting; ▶ Fire x Cutting;

■ Grazing x Cutting; ▪ Fire x Grazing; ● Fire x Cutting x Grazing

Species (axis 1):
- Andropogon gayanus
- Schizachyrium sanguineum
- Andropogon ascinodis
- Monocymbium ceresiiforme
- Chasmopodium caudatum
- Aspilia bussei
- Brachiaria jubata
- Hyparrhenia cyanescens
- Cochlospermum tinctorium
- Hyparrhenia diplandra
- Merremia hederacea
- Discoriste perrottetii
- Cassia mimosoides
- Lepidagathis anobrya
- Sporobolus microprotus
- Fimbristylis hispidula
- Indogofera leprieuri
- Tripogon minimis
- Andropogon pseudapricus
- Pandiaka heudelotii
- Euclasta condylotrichia
- Microchloa indica
- Loudetia togoensis
- Diheteropogon hagerupii
- Andropogon fastigiatus
- Elionurus elegans