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Examination of multiple disturbances effects on herbaceous vegetation communities in the Sudanian savanna-woodland of West Africa

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Abstract

In West Africa policies for prescribed early fire, grazing and selective tree cutting in the savanna-woodlands are rarely based on long-term experimental studies. The purpose of this study was to provide scientific evidence based on field data from two case studies for an informed discussion on the long-term response of herbaceous abundance both at the community and individual species levels to fire, grazing, selective cutting and their interactions. A long-term factorial experiment was established in two State forests reserve in Burkina Faso, and mainly differing in their soil attributes. Community abundance data recorded from line intercept sampling over 13 years, were analyzed using a multivariate ordination technique known as Principal Response Curves (PRC).

The results indicate that disturbance regimes, independently or interactively, influenced species abundance over time with inter-site specificity. The dynamics of these disturbance regimes exhibited temporal variation which could be related, to some extent, to inter-annual variation in annual rainfall. The PRC ordination accounted for 38% and 34% of the variation within the data set for sites with deep and shallow soils, respectively. At the site with deep soils, more than one PRC axis was needed to summarize the community response sufficiently, suggesting that the species reacted in different ways to disturbances. The PRC method approach to the analysis of disturbance dynamics allowed us to distil the complexity of the community responses to those of individual species and to identify species that can serve as indicators of certain disturbance regimes.

Keywords: Fire; herbivory; interactive disturbance; understory abundance; multivariate 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 treatment plots. From these large datasets, however, only information about a limited number of taxa (usually the most abundant ones) or overall means have, so far, been properly analyzed with standard univariate statistical methods (Savadogo et al., 2007; Sawadogo et al., 2005). Although such techniques are well documented and robust, in general they tend to explain about half of the variation, as is usual for multivariate analysis in vegetation studies (Grace, 1999). Previously, we applied repeated measures analysis, but it was not possible to discern treatment effects at the level of individual species (Savadogo, 2007). In order to obtain a complete picture of disturbance dynamics and their effect on the vegetation community, an appropriate multivariate analysis technique that combines the interaction between treatment and time effects, both at community and individual species levels is needed.

In this study, the main research question was: how do the effects of disturbance regimes on herbaceous vegetation abundance change over time? The research question could also be phrased: what is the response, over time, of the herbaceous vegetation community to fire, grazing and selective cutting disturbances? To answer these questions, the abundance of herbaceous vegetation recorded over 13 years (1994-2006) was analyzed using a multivariate ordination technique called Principal Response Curves (PRC). PRC analysis is an ordination method based on partial redundancy analysis and developed specifically for analysis of community response data from designed experiments sampled repeatedly over time (van den Brink and ter Braak, 1998; 1999). Associated with each PRC is a set of species weights, which reflect the influence of each species on the overall community response described by the PRC scores over time.

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 ≥10 cm GBH (girth at breast height). At Tiogo, the equivalent figures were 10.9 m^2 ha^{-1} at stump level, 6.1 m^2 ha^{-1} at breast height and 542 individuals ha^{-1}.

The unimodal rainy season lasts for about six months, from May to October. The mean (± SE) annual rainfall (Fig. 1) during the period (1994-2006) was 869 ± 39 mm for Laba and 848 ± 49 mm for Tiogo, and the number of rainy days per annum was 69 ± 5 and 66 ± 3 for Laba and Tiogo, respectively. Mean daily minimum and maximum temperatures are 16°C and 32°C in January (the coldest month) and 26°C and 40°C in April (the hottest month), yielding an aridity index (Brown and Lugo, 1982) of 3.5 and 3.7 for Laba and Tiogo, respectively. Most frequently encountered soils are Lixisols (Driessen et al., 2001), and the soil at Laba is shallow (< 45 cm depth) silty-sand while it is mainly deep (>75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998).

2.2 Experimental design

A factorial experiment was established in each of the two state forests to examine the effects of grazing, early fire, selective cutting and their interaction on abundance of herbaceous vegetation (Fig. 2). Each experimental site (18 ha) was divided into eight blocks (2.25 ha); four of which were fenced to exclude livestock (hereafter refereed to as non-grazed plots) and the other four were open for grazing (hereafter referred to as grazed plots). Each block was further divided into four plots of 0.25 ha (50 x 50 m), separated from each other by 20 – 30 m fire-breaks. To the four plots within each block, the following treatments were randomly assigned: No cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire. The selective cutting was done in December 1993 at Tiogo and a month later in January 1994 at Laba by removing 50% of the basal area at stump level. Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and fuelwood, and fuelwood and others (Hagberg et al., 1996; Sawadogo, 1996). Except protected species, individuals of other categories were cut according to the following size criteria: > 30 cm butt diameter for timber species, > 14 cm diameter at stump level for poles and fuelwood species and > 8 cm diameter at stump level for fuelwood and others (Sawadogo et al., 2002). The prescribed early fire was applied at the end of the rainy season (October – November) each year beginning 1993 when the grass layer humidity was approximately 40%. The grazing main plots at both study sites were open for grazing by livestock (a mixed herd of cattle, sheep and goats) mainly but also wild animals. The livestock carrying capacity in Laba forest 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} (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo et al., 2005). The presence of the livestock in the two forests varied spatially and temporally; grazing mainly occurs during the rainy season when grasses were green and surrounding area cultivated.

2.3 Data collection and analysis

The abundance of herbaceous vegetation was assessed every year from 1994 to 2006 at the end of the rainy season (September to October) when most of the species are flowering and fruiting, which allows for easy species identification. The point-intercept sampling procedure (Levy and Madden, 1933) was used to gather species-cover data. The presence of species was recorded along a 20 m permanent line laid in each subplot at an interval of 20 cm, giving a total of 100 sampling points. At each point record, a pin of 5 mm diameter taller than the maximum height of the vegetation was projected from above, and all contacts were recorded if the pin hit any of the live parts of a grass species. The positions of the transect lines were permanently marked to ensure accurate relocation each year. Identification of species and families of plants follows Hutchinson et al. (1954).

Initial data exploration to investigate the range of variation in the data set was carried out using detrended correspondence analysis (DCA), a method of indirect gradient analysis (ter Braak and Smilauer, 2002). However, the gradient length for the first axis was 1.05 and 1.33 for Tiogo and Laba, respectively, which are less than the recommended values, 3.0; thus species data set was ordinated with Principal Component Analysis (PCA). The abundance data for all herbaceous species (152 and 176 at Tiogo and Laba respectively) in response to fire, grazing, selective cutting and their interactions over the study period were then analyzed using Principal Response Curves (PRC) analysis. This technique is based on the ordination technique called partial redundancy analysis and developed specifically for analysis of community response data from designed experiments sampled repeatedly through time (van den Brink and ter Braak, 1998; 1999). Time coded as dummy variable was considered as covariable and only time by treatment interaction (also coded as dummy variable) were considered as explanatory variables. PRC plots the first principal component of the treatment effects against time, expressed as deviations from the control/reference treatment (van den Brink and ter Braak, 1998). The general model for the first principal component can be expressed as:

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

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 mean log-abundance of species *k* in year *t* in the control (*d* = 0), c_{dt} is the score of the *d*th treatment at year t, d_k is the weight of the *k*th species and $\varepsilon_{d(j)tk}$ is an error term with mean zero and variance σ_k^2. The coding used in the PRC standardized the control to be zero-valued ($C_{ot} = 0$) for all times i.e. horizontal line in the PRC diagram. Species abundance was $\ln(x+1)$-transformed to approximate the normal distribution while accounting for large number of zeros in the initial species data matrices, for which ln0 is undefined. In this case the reference (the control) was taken as the no fire + no cutting + no grazing plots. The underlying assumption for choosing this treatment as reference was that a system in undisturbed state is fairly stable and the effect of any disturbance can be gauged against this stable state. Associated with each PRC is a set of species weights, which reflect the influence of particular species on the overall community response described by the PRC scores over time. Species with high positive scores are positively correlated, species with negative scores respond oppositely, and species with near-zero scores are indifferent to the trend recognized by the PRC axes (ter Braak and Smilauer, 2002). The statistical significance of the resulting PRC axes was evaluated using Monte Carlo permutation tests ($p < 0.05$ after 499 permutations under split-plot constraints) by permuting freely data from the whole treatments within each year. Changes in treatment effects through time were evaluated in sequential tests for each sampling year by permuting the census data. Monte Carlo permutation test was also performed to determine the effects of each treatment separately in time, plus their interactions with other treatments. The statistical analyses were performed using the software package CANOCO 4.5 and the ordination diagrams drawn in CANODRAW (ter Braak and Smilauer, 2002).

3. Results

The initial ordination of the herbaceous vegetation using PCA showed a low degree of variation in the abundance of species between treatments averaged over the study period, as evidenced from the low eigenvalue for the first axis, which was 0.34 for Tiogo and 0.41 for Laba. The PCA score/loading biplot further showed a low affinity of species to particular treatment at both Tiogo (Fig. 3A) and Laba (Fig. 3B). Although species affinity to treatments appeared low, it was still difficult to visualize, quantify and test for treatment by year interactions within the classic ordination framework provided by PCA. It should be noted that we averaged the abundance across the study years in order to clearly see how the responses of individual species spread over the different treatments.

The PRC ordination accounted for 38% and 34% of the variation within the data set for Tiogo and Laba, respectively (Table 1). The PRC models for the first axis in the full data showed that 13% and 8% of the total variation were attributed to sampling years at Tiogo and Laba, respectively while treatment regime accounted for 25% and 26% of the total variation at Tiogo and Laba, respectively (Table 1). At both study sites, the first axis captured 25% to 35% of the total variation and was significant (Table 1). The second axis was also significant for Tiogo but not for Laba. The effects of each treatment separately in time, plus their interactions with other treatment indicated that the variation accounted for by the first axis ranged from 55% to 72% at Tiogo and 23% to 79%.at Laba (Table 1). At Tiogo, the first PRC axis was significant for all treatments and their interactions except grazing and fire × cutting treatment, while at Laba it was significant for cutting, fire × grazing and fire × cutting × grazing treatments. The PRC diagram for the first axis showed that there were two directions of departure from the control plots at Tiogo where fire, grazing and selective cutting were not applied (Fig. 4A). The main effects of fire, selective cutting and grazing on abundance were generally positive for the herbaceous vegetation community through out the study period; particularly these treatments favoured species, such as *Loudetia togoensis*, *Andropogon* *fastigiatus*, and *Andropogon pseudapricus*. The interaction effects were generally negative at community level compared to the control across the study period while having pronounced positive effects on species such as *Andropogon gayanus, Chasmopodium caudatum* and *Andropogon ascinodis*. Several species had their weight close to zero, indicating that they seemed insensitive to the treatments over time. The Monte Carlo tests per sampling year revealed that the treatment regimes had significant effects on herbaceous species abundance after 4 (1998), and 6-10 (2000-2004) years (Table 2). The PRC diagram also showed that the extent of the fire, selective cutting, and fire × cutting × grazing interaction effects was larger than the effects of grazing and other interactions as evidence from the large deviation of these lines from the control (Fig. 4A).

For the second axis, the PRC diagram revealed additional treatment effects as evidenced from a new set of species (Fig. 4B). The extent of fire and selective cutting main effects was larger than the oppositely oriented main effect of grazing, shown by the lines directed to the negative side of the vertical axis. Apparently, fire enhanced the abundance of *Andropogon ascinodis* and *Diheteropogon amplectens* throughout the study period, so also selective cutting during most of the study period. Among treatment interactions, cutting × grazing and fire × cutting × grazing had a larger positive influence on the abundance of species such as *Pennisetum pedicellatum* during most of the study period. Several other species also responded differentially to treatments during the study period as shown by their weights.

At the second case study site, Laba, the PRC analysis for the first significant axis revealed that the treatment effects over time deviated from the control bi-directionally where the main effects of fire, grazing and selective cutting are oriented in the negative side of the vertical axis while the interaction effects are oppositely oriented except grazing × cutting (Fig. 5). Fire strongly influenced the abundance of herbaceous species during the study period by favoring species such as *Elionurus elegans, Andropogon fastigiatus, Diheteropogon hagerupii* and *Loudetia togoensis* while disfavoring *Andropogon gayanus, Schizachyrium sanguineum, Andropogon ascinodis* and *Monocymbium ceresiiforme*. Grazing was the second most important factor affecting the abundance of herbaceous species over time followed by selective cutting. The extent of influence exerted by treatment interactions was generally small compared to main effects of fire and grazing. On the basis of Monte Carlo tests per sampling year, the treatment regimes had significant effects on herbaceous species abundance after 8-12 years (2002-2006) while marginally significant after 5 (1999) and 7 (2001) years (Table 2).

Summary of the test for each treatment effect over time for Tiogo is presented in Table 2A, and the pattern is graphically depicted in Fig. 4A. The main effect of fire was significant in 2002 where abundance of herbaceous vegetation was relatively low compared with the previous sampling years. The effect of grazing was significant during the last five years of sampling (2002-2006) where abundance was higher in these sampling years except 2003 when grazing resulted in reduced abundance compared to the other sampling years. Selective cutting had more positive effect on the abundance of herbaceous vegetation community in 1997, 1998 and 2004 than the rest of the sampling years. The interaction effect of fire × cutting was positive in 1994 and 2003 than the other sampling years when abundance was relatively lower than the control. The fire × grazing treatment had a decreasing effect on abundance for the sampling years 2001, 2003 and 2005 and an increasing effect in 2004. The abundance of the herbaceous vegetation generally decreased in cutting × grazing and fire ×

grazing × cutting plots through out the sampling years except 2003 in the former and in 2002 and 2003 in the latter when abundance was closer to the control.

Similar Monte Carlo tests results for the second case study site, Laba, is given in Table 2B, and the pattern of this inter-annual variation depicted in Fig. 5. The fire treatment resulted in significantly lower abundance in 2001 than in some of the sampling years (e.g. 1994, 1997, 2005), while grazing reduced the abundance of herbaceous vegetation during the last three years (2004-2006) compared with the previous years. The effects of selective cutting did not vary across sampling years. In fire × grazing treatment, the response of herbaceous vegetation was positive in 1995, 1998 and 2001-2006 while negative in 1994 and 1999. Abundance was lower in 2004 for fire × cutting treatment, in 2002-2006 for cutting × grazing and in all sampling years except 1995-1997 for fire × grazing × cutting treatment than the other sampling years.

4. Discussion

4.1 PRC model overview

The PRC model summarized the extensive species by sample data with one or two significant axes, depending on the case study site. Dimensional complexity is an important factor in the interpretation of multivariate analysis and models with few dimensions (axes) are often highly preferred. The proportion of variation accounted in the PRC ordination was higher for the treatment regime (involving time by treatment interaction) than for time for both study sites. This suggests that the treatment effects on species abundance were more important than the time per se. The fact that more than one PRC axis was needed to summarize the large data set from Tiogo suggests that the species reacted in quantitatively different ways to the treatments, as can be deduced from their weights.

4.2 Responses to individual treatments

The species composition of savanna ecosystems is maintained by a dynamic interaction between local colonization and local extinction due to competitive exclusion. In turn, these are influenced by disturbances, such as fire, herbivory and selective cutting (Breman and Kessler, 1995; Gibson and Brown, 1991; McNaughton, 1983). At the Tiogo study site, the effect of fire, selective cutting or grazing on the perennial grasses *Andropogon gayanus, Andropogon ascinodis* and *Schizachyrium sanguineum* in the herbaceous vegetation community was negative compared to the control, but not for the annual grass *Chasmopodium caudatum*. On the deep soils of Tiogo, these treatments tended to favour annual grass species and adversely affect perennial ones. Low intensity fire (such as early fire) enhances the colonization processes by inducing a flush of germination and flowering, a transient increase in overall productivity due to removal of litter that increases the availability of nutrients, space and light, as well as maintaining tussocks and increasing their cover by favouring the tillering of perennial grass (Garnier and Dajoz, 2001; Whelan, 1995). In contrast, recurrent fires may create unfavourable conditions for the germination of some species and can exhaust the below-ground reserves of perennials leading to their disappearance and replacement with more competitive annuals. In addition, post fire gaps may be drought-prone as a result of elevated evaporation that reduces moisture availability at the shallow depths where germination occurs, thus contributing to extinction processes (Elberse and Breman, 1990). The opposite effect was noted at the Laba study site: in the shallow soils at this site the perennial grass species *Andropogon gayanus, Schizachyrium sanguineum, Andropogn ascinodis, Monocymbium ceresiiforme* were favoured by the treatments while the annual grass species were adversely affected. The inter-site variability in the fire effect could be due to the occurrence of only short-lived fires at Laba because of the dominance of annual grass species with lower biomass compared to Tiogo where perennials dominate. The inter-site variability in fire effect could be due to relatively high fire intensity at Laba, which, in turn, is related to the increased availability of fuel in the form of biomass from annual grasses.

During the first half of the study period (1994-1999), the abundance of herbaceous vegetation increased somehow steadily in response to fire treatment, particularly at Tiogo. This initial increase may be related to increased availability of nitrogen and other nutrients essential for plant growth through deposition of ash (Jensen et al., 2001; Wan et al., 2001). The treatment effect was statistically significant (Monte Carlo tests) for 2001 at Laba and 2002 at Tiogo, which could be explained by interaction of fire with other environmental factors, such as rainfall. The mean annual rainfall was low for three consecutive years (2000-2002) at both study sites compared to the immediate sampling years before and after these years. Fire treatment might exacerbate drought in the post burn environment and resulted in reduced abundance of herbaceous vegetation. As a whole, the effect of fire on herbaceous vegetation community depends on growth form, fire frequency and intensity (Bennett et al., 2003; Sawadogo et al., 2005), and the latter in turn depends on fuel load, moisture content of the fuel and weather conditions (Goldammer, 1990; Scholes and Walker, 1993).

The species composition and abundance of the understory increases following the formation of canopy gaps created by tree removal; this is due to reduced competition for water and nutrients as well as increased availability of light and growing space (Akpo et al., 2003; Frost et al., 1986). There is evidence of this in the first PRC diagram for the Tiogo study site, where abundance increased steadily during the first five years of the study period. In contrast, at

Laba the effect of selective cutting on the abundance of herbaceous vegetation over time was slightly negative. This could be related to drought effects, exacerbated by the selective removal of trees at Laba where the soil is mainly shallow, silty-sand with a low water holding capacity. It is indeed expected that the canopy gaps created by selective removal of trees may create unfavourable thermal conditions in arid and semi-arid areas and favour the growth of drought-tolerant species only, thereby contributing to competitive exclusion process.

Although grazing had a positive effect on the herbaceous vegetation community during the study period, the extent of its effect was lower than that of fire or selective cutting at Tiogo. The grazing intensity in our subplots, particularly at Tiogo, was half the carrying capacity (Sawadogo, 1996), thus many species could survive intermediate levels of grazing that allows succession to proceed but limits the ability of a few highly competitive species to dominate the community. Generally, moderate grazing enhances plant diversity through enhanced propagule dispersal, increased availability of light, and improving soil conditions while reducing local extinction rates by preferentially consuming competitive, dominant plants (Olff and Ritchie, 1998). The dynamics of grazing effects during the course of the study period are, in fact, related to the spatio-temporal variation in stocking rate and grazing intensity, which are common in the Sahel region (Hiernaux, 1998). At Laba, grazing had a greater negative impact at community level during the study period. This negative effect could be a consequence of the low biomass production at this site (Sawadogo et al., 2005) coupled with heavier grazing pressure (Sawadogo, 1996) than at Tiogo.

4.3 Responses to treatment interactions

Generally all treatment interactions had a negative effect on the herbaceous vegetation community at Tiogo site during most of the study period. Their effects, however, were positive (increasing abundance) for perennial grass *Andropogon gayanus, Andropogon ascinodis* and *Schizachyrium sanguineum.* The fire × cutting × grazing treatment effect was more pronounced than the other interaction effects. The removal of trees in 1994 created more growing space and probably enhanced the abundance of herbaceous vegetation. The increased availability of forage, in turn, might attract more herbivores and/or resulted in intense fire that eventually decreased the abundance of herbaceous species. The negative effect of this treatment interaction slightly fluctuated across the sampling years until 2002 and 2003 when abundance increased significantly closer to the control. This dynamics can be explained by the gradual decrease in the positive effect of selective cutting (increased growing space and reduction of competition) due to rapid colonization during the first few years (as can be seen from steady-state increase in selectively cut plots), which in turn reduced the availability of fuels and fire intensity. From the PRC diagram (Fig. 4A) it appears that the extent of selective cutting × grazing effect was more pronounced than the effect of fire × cutting or fire × grazing. This indicates high grazing pressure and stocking rate in response to abundance of forage following selective removal of trees, which might be the reason for limited effect of this treatment over the study period. Contrary to Tiogo, treatment interactions resulted in higher abundance of herbaceous vegetation community relative to the control during most of the study years, except cutting × grazing treatment. This site-specificity could be partly explained by the spatial distribution of herbaceous species at each case study site. At Laba, 12 dominant species responded positively for treatment combinations than 4 dominant species at Tiogo (c.f. Fig. 4A and 5).

4.4 Methodological importance

Analysis of large scale studies on disturbance dynamics is often centred around the use of conventional statistical methods, such as analysis of variance (Sawadogo et al., 2005) or repeated measures analysis (Savadogo, 2007) based on data pooled over time or data from just a few individual species. Such analyses fail to reflect how the effects of disturbance vary over time or they do not allow the interpretation of results simultaneously at both community and individual species levels. PRC is a method for the visualization of results of repeated measurements analysis, focusing on time-dependent treatment effects (van den Brink and ter Braak, 1998; 1999). It has the capacity to reveal trends at a major community level within a large data matrix, combined with an increased ecological relevance to studies at lower levels of biological organization (Kedwards et al., 1999). PRC analysis has been successfully used in a variety of applications ranging from ecotoxicological field studies (Kedwards et al., 1999; van den Brink and ter Braak, 1998; 1999), climate change effects (Frampton et al., 2000; Heegaard and Vandvik, 2004; Vandvik, 2004), vegetation and disturbance dynamics (Britton and Fisher, 2007; Francisco et al., 1995; Kohler et al., 2006; Pakeman, 2004; Pakeman et al., 2003; Vandvik, 2004; Vandvik et al., 2005) to the effects of ecosystem type (Neher et al., 2005) and agricultural management regime (Salles et al., 2006). In all these applications PRC appears to be a powerful tool for analyzing community responses to different perturbations over time than the conventional univariate methods and multivariate ordination techniques (e.g. DCA). Compared to our previous results based on repeated measures analysis of variance (Savadogo, 2007), PRC enabled us to interpret treatment effects not only at the community level but also at the individual species level. Such information is indispensable for identifying species that can serve as indicators of particular disturbance regimes. For example, Leps & Smilauer (2003) demonstrated the potential value of multivariate methods for identifying indicator species or taxa, the abundance of which may be indicative of particular environmental variables or experimental treatments. Since species with the highest weights in PRC analysis are most likely follow the overall community response, species weight may be used to identify potential indicator species. In our study, *L. togoensis*, *A. gayanus*, *A. fastigiatus*, *A. ascinodis*, *C. caudatum* and *Pennisetum pedicellatum* have the highest weights at Tiogo, while *A. gayanus*, *A. fastigiatus*, *Elionurus elegans* and *Schizachyrium sanguineum* have the highest weights at Laba. Thus, these species could potentially serve as indicators of fire, grazing and selective cutting disturbances in the Sudanian savanna woodland. The limitations of this technique should be mentioned as well. This method assigns a single weight to each species suggesting that their relative importance does not change over time contrary to the fact that the treatments applied in this experiment may generate processes with changing nonlinear contributions (weights) of species.

Conclusions

This study illustrates that the herbaceous vegetation component of savanna-woodland responds differently along a time gradient to single or combined disturbances of fire, grazing and tree removal. Furthermore these effects are site-specific, suggesting that their effects interact with other environmental factors such as soil characteristics. The dynamics of these disturbance regimes also interact, to some extent, with rainfall. The PRC approach to the analysis of disturbance dynamics in this study appears to be indispensable, in that it allows identification of potential indicator taxa that could be used for monitoring the effects of disturbance regimes on the herbaceous community in savanna-woodlands.

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

		Data subset						
	Full data set	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

		Data subset						
	Full data set	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.

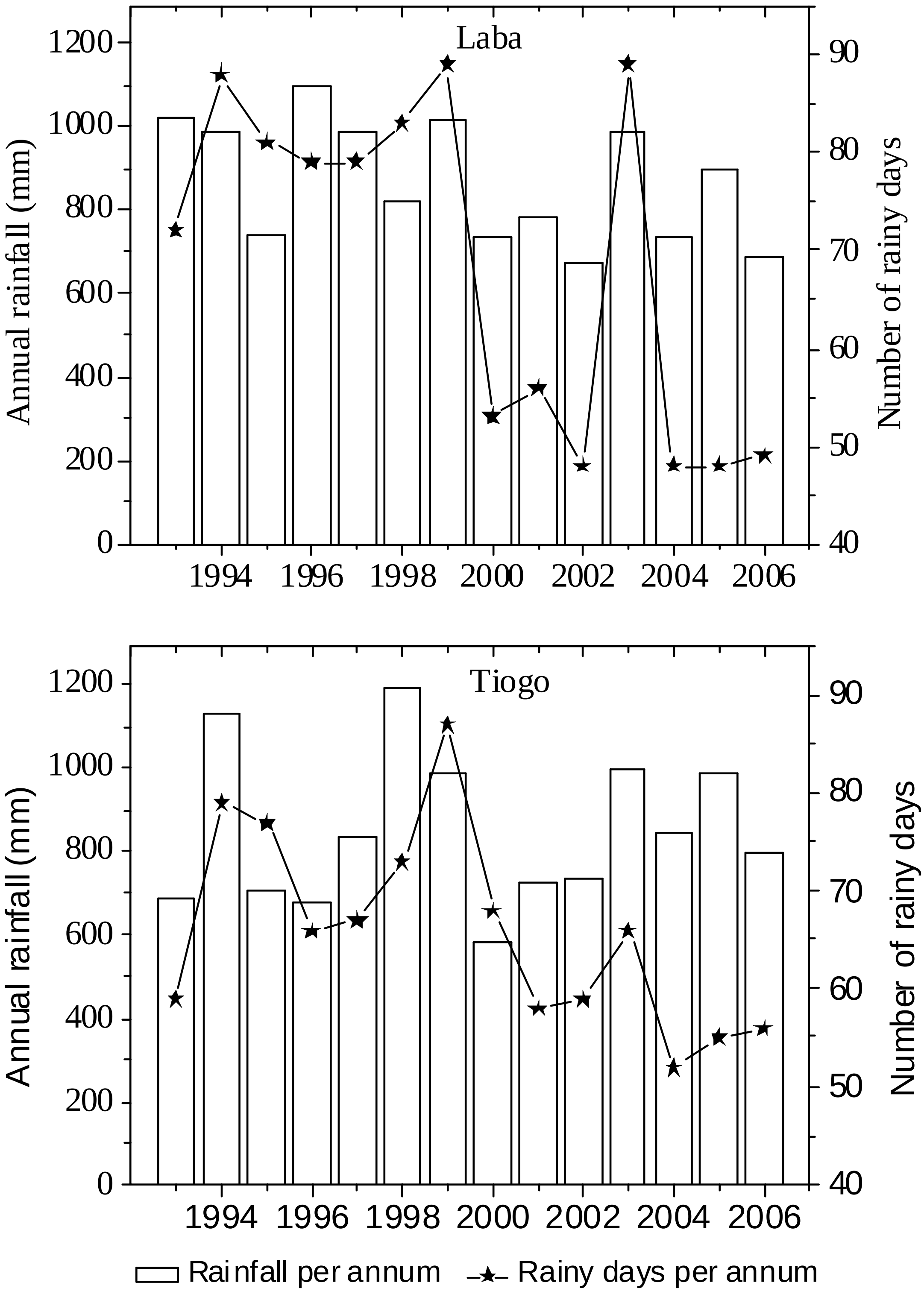
Fig. 3. PCA biplots of an ordination of species by treatment regimes for two case study sites (A for Tiogo and B for Laba). A complete list of species is given in the appendix and the treatment regimes abbreviated as follows: F = fire, G = grazing, C = selective cutting, FG = fire × grazing, FC = fire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



Laba
Annual rainfall (mm)
0
200
400
600
800
1000
1200
Number of rainy days
40
50
60
70
80
90
1994
1996
1998
2000
2002
2004
2006
Tiogo
Annual rainfall (mm)
0
200
400
600
800
1000
1200
Number of rainy days
40
50
60
70
80
90
1994
1996
1998
2000
2002
2004
2006
Rainfall per annum
Rainy days per annum

Fig. 2.

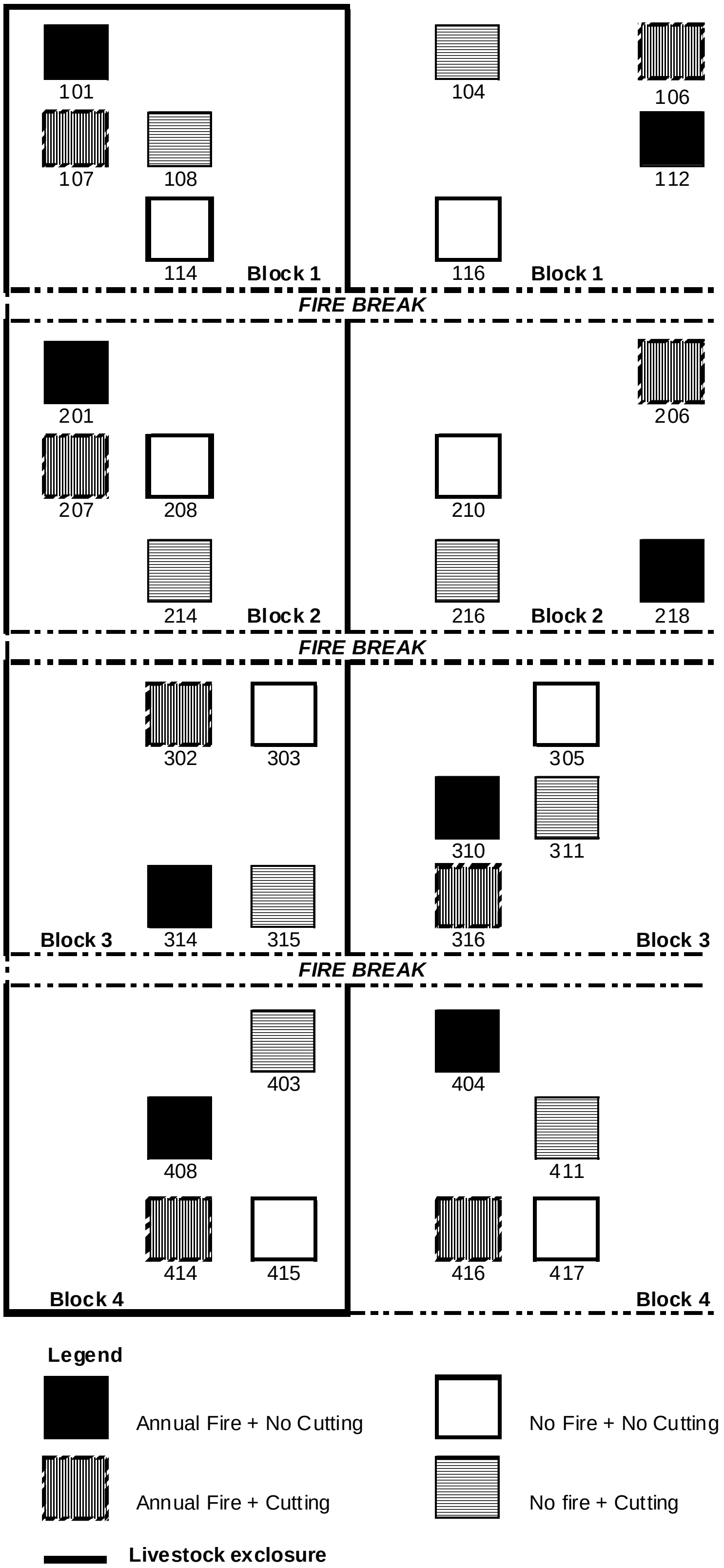
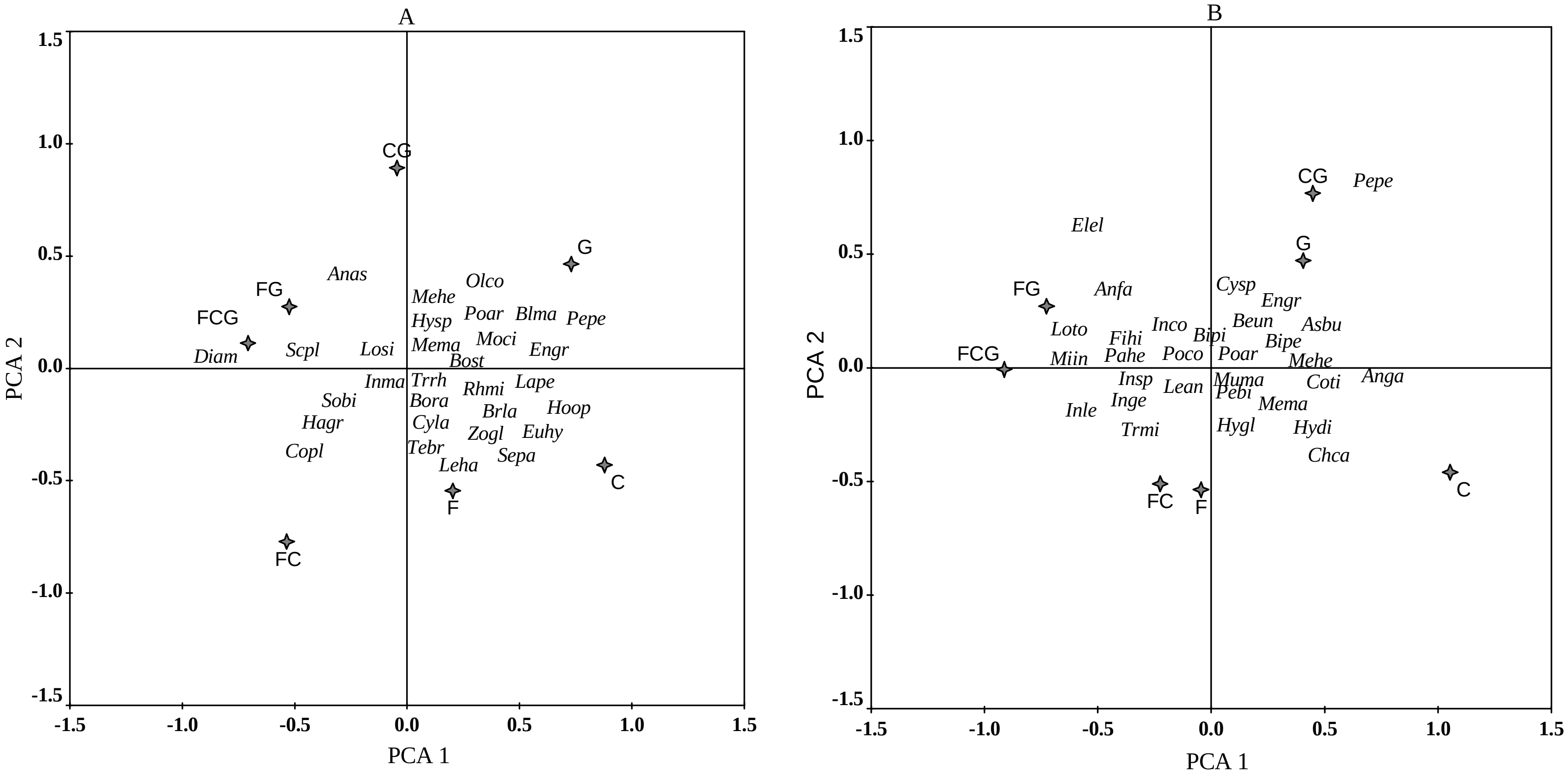
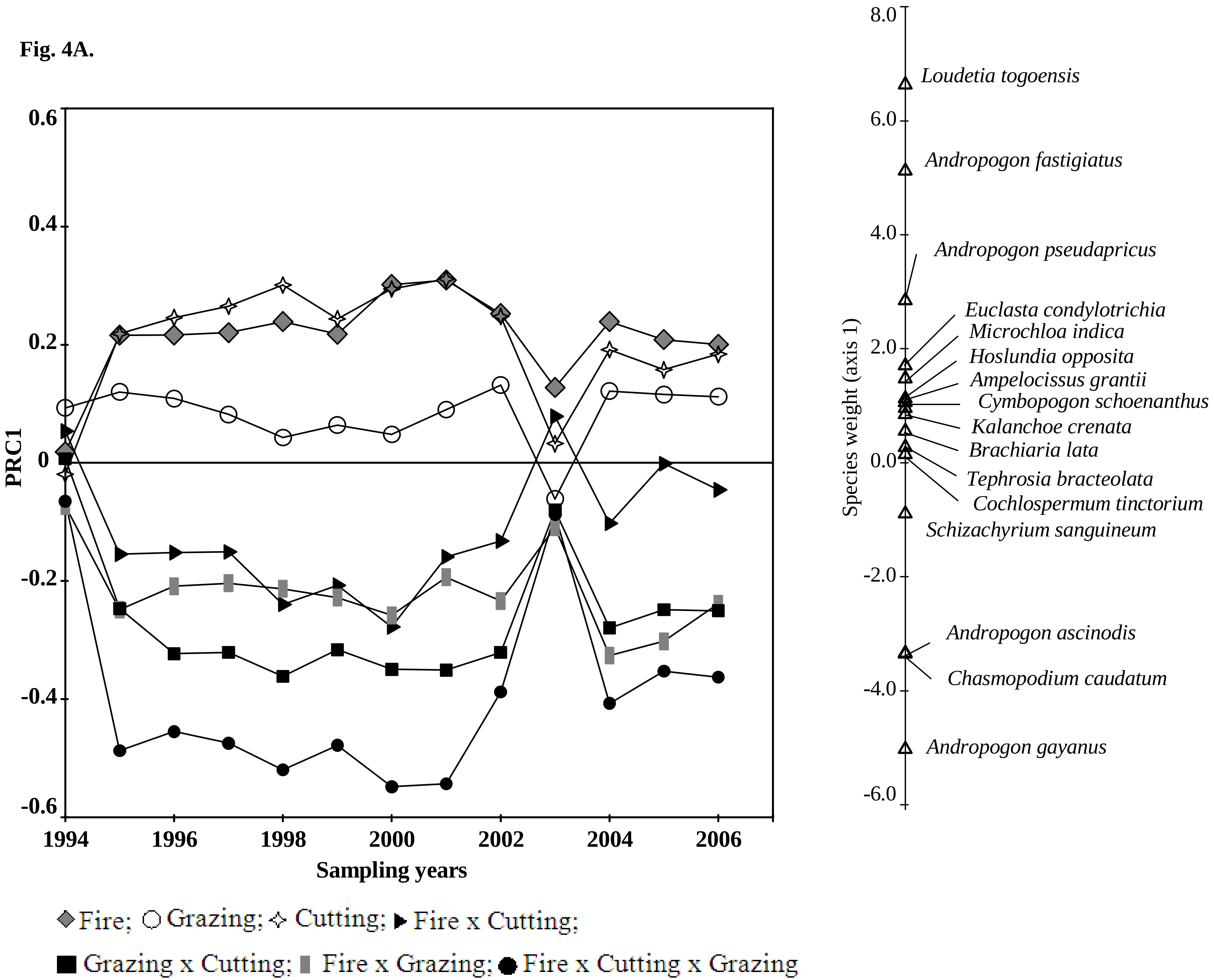

101
104
106
107
108
112
114
Block 1
116
Block 1
FIRE BREAK
201
206
207
208
210
214
Block 2
216
Block 2
218
FIRE BREAK
302
303
305
310
311
314
315
316
Block 3
Block 3
FIRE BREAK
403
404
408
411
414
415
416
417
Block 4
Block 4
Legend
Annual Fire + No Cutting
No Fire + No Cutting
Annual Fire + Cutting
No fire + Cutting
Livestock exclosure

Fig. 3.



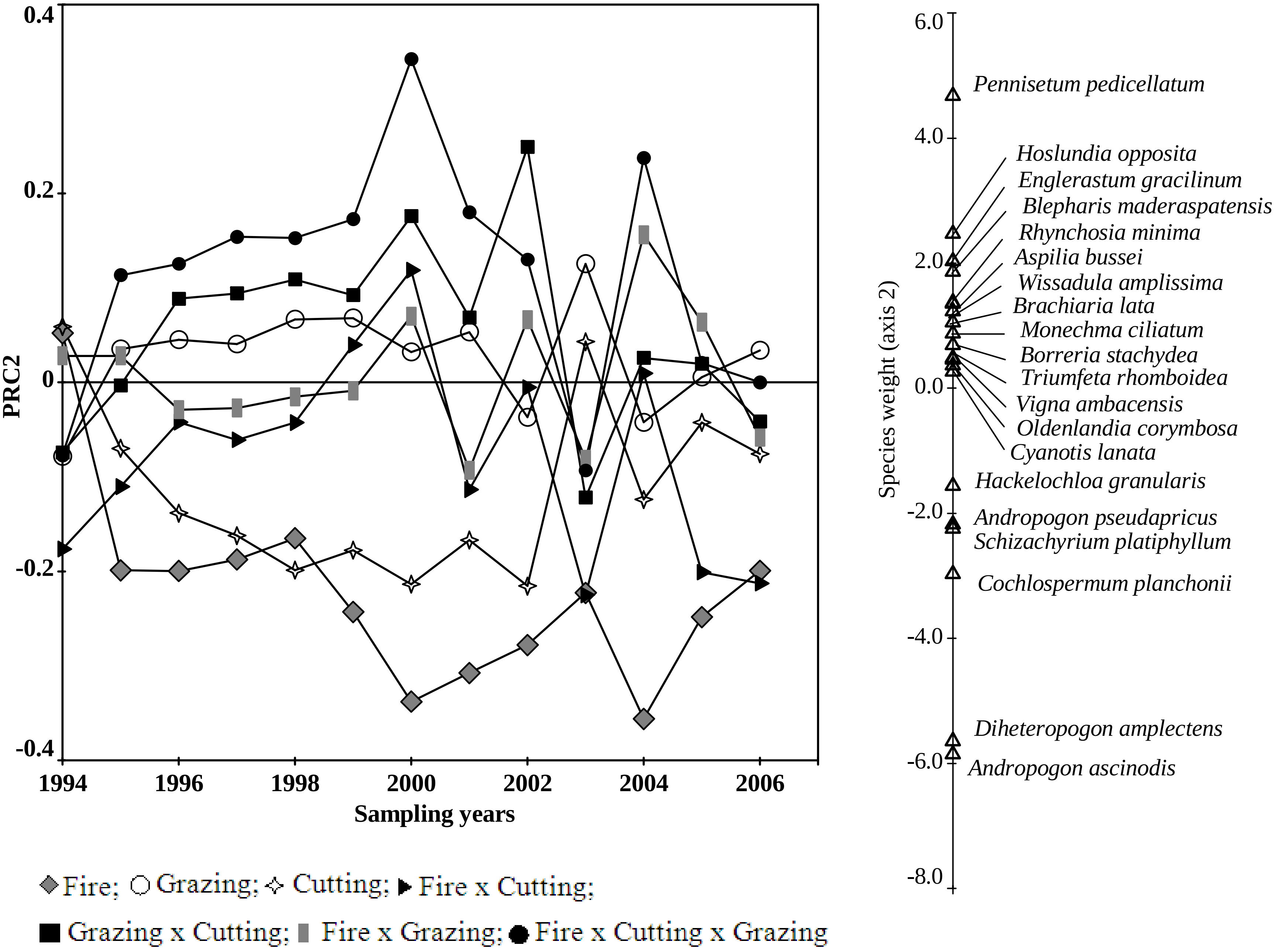
A
B
PCA 1
PCA 2
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
CG
G
FG
FCG
FC
F
C
Anas
Olco
Mehe
Hysp
Poar
Blma
Pepe
Mema
Moci
Engr
Bost
Diam
Scpl
Losi
Inma
Trrh
Rhmi
Lape
Sobi
Bora
Brla
Hoop
Hagr
Cyla
Zogl
Euhy
Copl
Tebr
Sepa
Leha
Elel
Anfa
Cysp
Loto
Inco
Beun
Asbu
Fihi
Bipi
Bipe
Miin
Pahe
Poco
Muma
Anga
Insp
Lean
Pebi
Coti
Inle
Inge
Trmi
Hygl
Hydi
Chca

Fig. 4A.



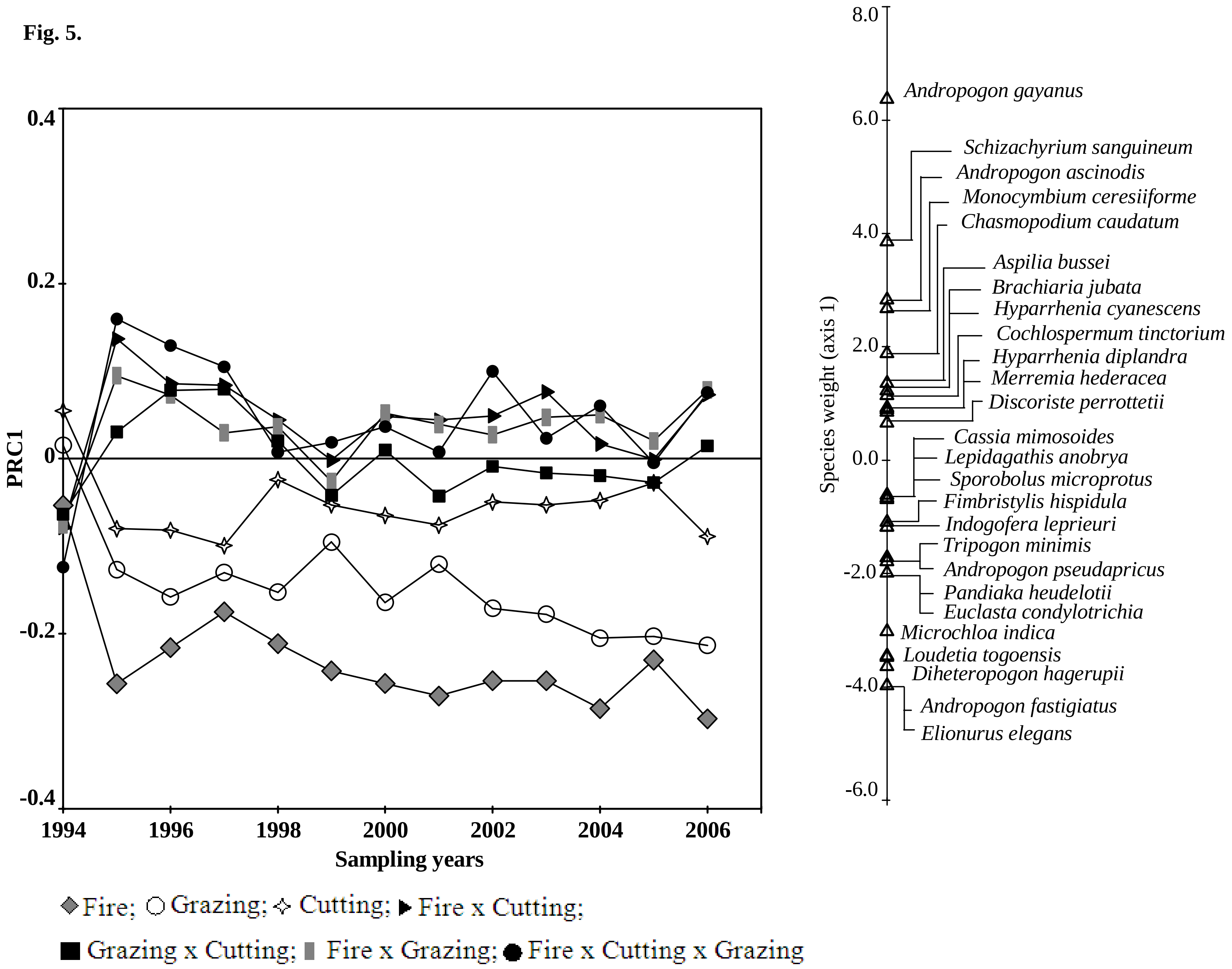
PRC1
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
1994
1996
1998
2000
2002
2004
2006
Sampling years
◆ Fire; ○ Grazing; ✧ Cutting; ▶ Fire x Cutting;
■ Grazing x Cutting; ▮ Fire x Grazing; ● Fire x Cutting x Grazing
Species weight (axis 1)
8.0
6.0
4.0
2.0
0.0
-2.0
-4.0
-6.0
Loudetia togoensis
Andropogon fastigiatus
Andropogon 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.



PRC2
0.4
0.2
0
-0.2
-0.4
1994
1996
1998
2000
2002
2004
2006
Sampling years
Species weight (axis 2)
6.0
4.0
2.0
0.0
-2.0
-4.0
-6.0
-8.0
Pennisetum pedicellatum
Hoslundia opposita
Englerastum gracilinum
Blepharis maderaspatensis
Rhynchosia minima
Aspilia bussei
Wissadula amplissima
Brachiaria lata
Monechma ciliatum
Borreria stachydea
Triumfeta rhomboidea
Vigna ambacensis
Oldenlandia corymbosa
Cyanotis lanata
Hackelochloa granularis
Andropogon pseudapricus
Schizachyrium platiphyllum
Cochlospermum planchonii
Diheteropogon amplectens
Andropogon ascinodis
◆ Fire; ○ Grazing; ✧ Cutting; ▶ Fire x Cutting;
■ Grazing x Cutting; ▮ Fire x Grazing; ● Fire x Cutting x Grazing

Fig. 5.



0.4
0.2
0
-0.2
-0.4
PRC1
1994
1996
1998
2000
2002
2004
2006
Sampling years
◆ Fire; ○ Grazing; ✧ Cutting; ▶ Fire x Cutting;
■ Grazing x Cutting; ▮ Fire x Grazing; ● Fire x Cutting x Grazing
8.0
6.0
4.0
2.0
0.0
-2.0
-4.0
-6.0
Species weight (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